

A NUMERICAL-TAXONOMIC STUDY OF THE SUBTRIBE NASSAUVIINAE (COMPOSITAE, MUTISIEAE)

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PLANTS BELONGING TO GENERA of the subtribe Nassauviinae (Compositae, Tribe Mutisieae) are an important component of the Andean flora of South America. Several species of Nassauviinae are dominant elements of extended areas, such as *Nassauvia axillaris* in Patagonia; *Proustia cuneifolia* in the phytogeographical region of Prepuna (Cabrera, 1971c), and *Proustia ilicifolia* in the Mediterranean region of Chile.

Several genera of the subtribe have been monographed recently, among them *Panphalea* [as *Pamphalea*] (Cabrera, 1953a), *Proustia* (Fabris, 1968), and *Perezia* (B. S. Vuilleumier, 1969). The arrangement of the genera in the subtribe, however, is very unclear. This has prompted me to undertake the present study, because I thought that numerical techniques could profitably be applied to quantify the taxonomic distances between the genera.

The limits of the genera of the Nassauviinae have been determined on the basis of my personal knowledge and published works on the subtribe by others. Two unresolved problems remain after following this procedure; first, a number of species continue to be hard to place in the classically accepted genera, and second, the relationship between the genera is still uncertain.

This paper reports the results of a numerical study undertaken in an attempt to solve these problems.

CONCEPT OF GENUS

Generic concepts have recently been discussed from various points of view by several biologists, notably Anderson (1940), Greenman (1940), Bartlett (1940), Camp (1940), Sherff (1940), Lawrence (1953), Bailey (1953), Eames (1953), Cave (1953), Mason (1953), Rollins (1953), Tutin (1956), Stebbins (1956), Cain (1956), Anderson (1957), Michener (1957), Inger (1958), Solbrig (1960), Simpson (1961), Löve (1963), Rosen and Bailey (1963), Davis and Heywood (1963), Kirpicznikov (1968), Mayr (1969), and Legendre and Vaillancourt (1969). Nevertheless, a few points might be pertinent to the problem under consideration. They also will illustrate my ideas about these matters and the underlying principles of this work.

Definition of any taxonomic category is very difficult, but probably no taxonomic category causes as much difficulty as the genus. Since there is no operational definition available, one is forced to adopt a pragmatic definition: the genus is the lowest higher category and the lowest of all

categories established strictly by comparative data; it may contain a single species, or a monophyletic group of species; it is separated from other taxa of the same rank (other genera) by a decided gap (Cain, 1956; Mayr, 1969).

There are no taxonomic characters which prove generic distinctness. Characters useful in one family for delimitation of genera may be useful in other families only for delimiting sections or species, or they may have no taxonomic value.

Recognition of a genus is generally based on the occurrence of correlated character complexes.

Delimitation of genera is largely determined by an author's concepts and is therefore somewhat subjective. It also is likely to be influenced by traditional usage in a particular family.

In the Compositae the tendency has been to distinguish many genera. In a family as large and homogeneous as this one, it is difficult to obtain a good understanding of large genera, e.g., *Senecio*, *Haplopappus*, *Baccharis*, *Solidago*, etc., while smaller groups (which are not necessarily too small) can be better understood. Furthermore, "small" genera are more likely to represent natural groups, that is to say, phylogenetic units.

The criteria used in this paper to determine generic limits in the Nassauviinae are the following: each genus should be (1) internally homogeneous; (2) separated from the other genera by a discontinuity (gap); (3) consistent with the evolutionary concept (phylogenetic units); and (4) consistent with the traditional usage of the concept of genus in the family Compositae. If after use of these criteria there were several alternate ways of delimiting the genera, the same principles were used as in the recognition of any scientific theory: "Where alternatives are available, we stand by the theory or concept that is most useful, the one that generalizes the most observations, and permits the most reliable predictions" (Inger, 1958: 383).

Finally the subtribe Nassauviinae serves as another example of Stebbins's (1956: 242) observations: "They make it impossible for us to erect a system of genera in which all intergeneric gaps have the same degree of validity from the standpoint of interspecific relationships."

In the manner presented above, the limits of the genera of Nassauviinae have been determined on the basis of the criteria described. Twenty-two genera were accepted. Four species of uncertain parentage were difficult to place in these genera, and for the purposes of this paper these critical taxa were treated as monotypic genera.

Each of the 26 "genera" was considered to be a basic unit possessing a "pool" of characters. In reality each genus includes one or more species and each species is composed of a number of populations, but in this case all taxa below the rank of genus contributed independently to that "pool." The boundaries of our units are the generic boundaries, and we considered each of these units potentially able to produce any of the characters that its components (species) have.

Macrachaenium, *Proustia*, *Lophopappus*, and *Calopappus* were included

TABLE 1. List of Revisionary Studies of Genera Currently included in the subtribe Nassauviinae.

GENUS	REVISIONARY STUDIES
PEREZIA Lagasca	B. S. Vuilleumier (1969)
ACOURTIA D. Don	Bacigalupi (as <i>Perezia</i> section <i>Acourtia</i> , 1931)
NASSAUVIA Commerson ex Jussieu	Cabrera (partial, 1971)
TRIPTILION Ruiz & Pavon	Crisci (in preparation)
LEUCHERIA Lagasca	Crisci (in preparation)
MOSCHARIA Ruiz & Pavon	Crisci (1974b)
OXYPHYLLUM Philippi	monotypic
POLYACHYRUS Lagasca	Ricardi (in preparation)
MARTICORENIA Crisci	monotypic
LEUNISIA Philippi	monotypic
MACRACHAENIUM Hooker f.	monotypic
PLEOCARPUS D. Don	monotypic
JUNGIA Linnaeus f.	Cerrate (partial, 1951)
TRIXIS Browne	Cabrera (partial, 1936), Loja (partial, 1969), Anderson (partial, 1972).
AMEGHINOIA Spegazzini	monotypic
DOLICHLASIUM Lagasca	monotypic
PANPHALEA Lagasca	Cabrera (1953a)
HOLOCHEILUS Cassini	Cabrera (1968)
LOPHOPAPPUS Rusby	Cabrera (1953b)
PROUSTIA Lagasca	Fabris (1968)
CEPHALOPAPPUS Nees & Martius	monotypic
CALOPAPPUS Meyen	Crisci (in preparation)

among the 22 genera accepted, but some authors have placed these four genera in other subtribes of the Mutisieae.

Both *Proustia* and *Macrachaenium* have sometimes been placed in the Mutisiinae (Hoffmann, 1893; Cabrera, 1961) because of their rounded styles. But for each genus the presence of flowers with bilabiate corollas, tailed anthers, and the type of exine stratification show that its position in Nassauviinae is not unnatural. Species of *Lophopappus* also have rounded styles and in some there are 5-partite corollas, characters which have led Cabrera (1961) to place this genus in an uncertain position (Mutisiinae or Gochnatiinae), but the presence of predominantly bilabiate corollas, tailed anthers, and the exine stratification again indicate *Lophopappus* is best placed in Nassauviinae.

De Candolle (1838) was the only author who excluded the genus *Calopappus* from the Nassauviinae, but its truncate style, bilabiate corollas, tailed anthers, and the exine stratification indicate *Calopappus* is also best placed in Nassauviinae.

METHODS

A thorough search of the literature on the morphology, phytogeography, and taxonomic history of the subtribe and of each group was undertaken.

TABLE 2. Chromosome numbers of members of the subtribe Nassauviinae.

TAXON	<i>n</i>	<i>2n</i>	REFERENCES
ACOURTIA (sub <i>Perezia</i> sect. <i>Acourtia</i>)			
<i>A. microcephala</i>		54	Raven, P. (ex Vuilleumier, B. S. 1969).
<i>A. thurberii</i>		54	Vuilleumier, B. S. 1969.
<i>A. nudicaulis</i>	28		Powell, M., <i>et al.</i> [in press].
HOLOCHEILUS			
<i>H. pinnatifidus</i> (sub <i>Trixis</i> <i>pinnatifida</i>)	11		Coleman, J. R. 1968.
JUNGIA			
<i>J. paniculata</i>		36	Diers, L. 1961.
MOSCHARIA			
<i>M. pinnatifida</i>	20		Crisci, J. V. unpublished.
LEUCHERIA			
<i>L. suaveolens</i>	20		Moore, D. 1967.
<i>L. hahnii</i>	19 & 20		Moore, D. unpublished.
<i>L. thermarum</i>	20		Crisci, J. V. unpublished.
<i>L. glacialis</i>	20		Crisci, J. V. unpublished.
<i>L. millefolium</i>	20		Crisci, J. V. unpublished.
<i>L. rosea</i>	20		Crisci, J. V. unpublished.
<i>L. runcinata</i>	20		Crisci, J. V. unpublished.
<i>L. achillaeifolia</i>	19 or 20		Crisci, J. V. unpublished.
MARTICORENIA			
<i>M. foliosa</i>	22		Crisci, J. V. 1974.
NASSAUVIA			
<i>N. darwinii</i>	11		Moore, D. unpublished.
<i>N. gaudichaudi</i>	22		Moore, D. 1967.
<i>N. magellanica</i>	11		Moore, D. unpublished.
<i>N. serpens</i>	11		Moore, D. 1967.
PEREZIA			
<i>P. multiflora</i>		16	Diers, L. 1961; Vuilleumier, B. S. 1969. Sneider (ex B. S. Vuilleumier, 1969).
<i>P. squarrosa</i> subsp. <i>cubaetensis</i>	4		Coleman, J. R. 1968.
<i>P. pungens</i>		24	Heiser, C. 1963.
<i>P. ciliaris</i>		24	Vuilleumier, B. S. 1969.
<i>P. carduncelloides</i>	12		Sneider (ex B. S. Vuilleumier, 1969).
<i>P. ciliosa</i>		24	Vuilleumier, B. S. 1969.
<i>P. calophylla</i>		24	Vuilleumier, B. S. 1969.
<i>P. coerulescens</i>		24	Vuilleumier, B. S. 1969; Diers, L. 1961.
<i>P. recurvata</i>		24 or 26	Vuilleumier, B. S. 1969.
<i>P. recurvata</i>	12		Moore, D. unpublished.
<i>P. magellanica</i>		24	Moore, D. unpublished.
<i>P. pilifera</i>		16	Moore, D. unpublished.

TABLE 2. Chromosome numbers of members of the subtribe Nassauviinae.
(continued)

TAXON	<i>n</i>	<i>2n</i>	REFERENCES
PROUSTIA			
<i>P. ilicifolia</i>		54	Covas, G., & B. Schnack, 1946.
TRIXIS			
<i>T. californica</i>	27		Turner, B. L., <i>et al.</i> 1962. Powell, M., <i>et al.</i> [in press]. Powell, M., & B. L. Turner, 1963.
<i>T. radialis</i>	27		Turner, B. L., <i>et al.</i> 1962. Powell, M., <i>et al.</i> [in press].
<i>T. paradoxa</i>		54	Diers, L. 1961.
<i>T. nelsonii</i>	27		Powell, M., <i>et al.</i> [in press].
<i>T. inula</i>	27		Raven, P. (ex C. Anderson, 1972).
<i>T. inula</i>		47 ± 3	Turner, B. L., <i>et al.</i> (ex C. Anderson, 1972).
<i>T. antimenorrhoea</i> var. <i>discolor</i>	27		Powell, M., <i>et al.</i> [in press].

These data were augmented by morphological studies of the genera based on herbarium material. All the organs were boiled in water before observation. Some pollen grains were acetolized (Erdtman, 1960), other pollen grains were placed in 95 per cent ethanol with basic fuchsin and mounted in glycerine jelly. The styles were treated with cloral-hydrate for 24 to 48 hours. Other styles were examined with a Scanning Electron Microscope (SEM). Taken directly from the herbarium material, the styles were placed on specimen holders, then coated with 50 Å to 100 Å carbon and about 200 Å to 300 Å gold-palladium alloy for conductivity. Finally the specimens were photographed using high resolution SEM, AMR model 900.

The abbreviations for herbaria are taken from the fifth edition of the Index Herbariorum (Lanjouw & Stafleu, 1964).

The computational work was done in an IBM system 360-70, at the Computing Center of the Office of Information Technology of Harvard University.

NUMERICAL TECHNIQUES

Twenty-six OTU's (Operational Taxonomic Units, *vide* Sneath & Sokal, 1973), including 22 genera and 4 critical taxa, were accepted.

Data accumulation. All characters used were qualitative or transformed to it and divided into their possible states (e.g., character: flower

color; states: blue, red, yellow, etc.). Each one of these states was scored for presence (1) or absence (0). The decision to score the states of the characters in this way was governed in part by the requirements of the logic of the work, which deals with units (genera) able (*or not*) to produce more than one state in one OTU.

In some cases such as: "receptacle pubescent (1) or not (0)" it is found that some genera include both species with pubescent receptacle and species with glabrous receptacle. It is clear that one state will not be enough to cover the possibilities and for this reason it was scored in the following way:

- receptacle pubescent (1) or not (0)
- receptacle glabrous (1) or not (0)
- receptacle glabrous *and* pubescent (1) or not (0)

This seems to be logically acceptable and a better presentation of the real situation.

The characters' states were scored for each OTU as follows:

- (1) Pappus paleaceous (1) or not (0).
- (2) Pappus setose (1) or not (0).
- (3) Pappus plumose (1) or not (0).
- (4) Pappus in one series (1) or not (0).
- (5) Pappus white (1) or not (0).
- (6) Pappus white *and* colored (1) or not (0).
- (7) Pappus colored (1) or not (0).
- (8) Involucre campanulate (1) or not (0).
- (9) Involucre hemispherical (1) or not (0).
- (10) Involucre cylindrical (1) or not (0).
- (11) Involucre turbinate (1) or not (0).
- (12) Involucre with 1 to 2 rows of bracts (1) or not (0).
- (13) Involucre with 1 to 2 *and* 3 to 7 rows of bracts (1) or not (0).
- (14) Involucre with 3 to 7 rows of bracts (1) or not (0).
- (15) Involucre with more than 5 bracts (1) or not (0).
- (16) Involucre with foliaceous bracts (1) or not (0).
- (17) Involucre with foliaceous *and* nonfoliaceous bracts (1) or not (0).
- (18) Involucre with nonfoliaceous bracts (1) or not (0).
- (19) Involucral bracts with wings (1) or not (0).
- (20) Involucral bracts with spines (1) or not (0).
- (21) Involucral bracts dimorphic (1) or not (0).
- (22) Involucre more than 3 mm. high (1) or not (0).
- (23) Involucral bracts with mucro (1) or not (0).
- (24) Involucral bracts with *and* without mucro (1) or not (0).
- (25) Involucral bracts without mucro (1) or not (0).
- (26) Inflorescence solitary (1) or not (0).
- (27) Inflorescence a cyme or panicle (1) or not (0).
- (28) Inflorescence a glomerulum or pseudocephalium (1) or not (0).
- (29) Capitula sessile (1) or not (0).
- (30) Capitula subsessile (1) or not (0).
- (31) Capitula with pedicel (1) or not (0).
- (32) Pollen grains prolate (1) or not (0).
- (33) Pollen grains subprolate (1) or not (0).
- (34) Pollen grains spheroidal-prolate (1) or not (0).

- (35) Pollen grains oblate (1) or not (0).
- (36) Colpi membrane with sexine process (1) or not (0).
- (37) Pollen grains with polar elevations (1) or not (0).
- (38) Exine Oxyphyllum-a type (1) or not (0) [see text].
- (39) Exine Oxyphyllum-b type (1) or not (0).
- (40) Exine Trixis type (1) or not (0).
- (41) Exine Proustia type (1) or not (0).
- (42) Exine Cephalopappus type (1) or not (0).
- (43) Exine Nassauvia remyana type (1) or not (0).
- (44) Present in West Indies (1) or not (0).
- (45) Present in Andes of South America, Patagonia (1) or not (0).
- (46) Present in South Brazil, Uruguay, Paraguay, NE of Argentina (1) or not (0).
- (47) Present in tropical South America (1) or not (0).
- (48) Present in Central and North America (1) or not (0).
- (49) Leaves entire (1) or not (0).
- (50) Leaves entire *and* partite (1) or not (0).
- (51) Leaves partite (1) or not (0).
- (52) Leaves with spines (1) or not (0).
- (53) Leaves with *and* without spines (1) or not (0).
- (54) Leaves without spines (1) or not (0).
- (55) Lower leaves sessile (1) or not (0).
- (56) Leaves six times or more longer than wide (1) or not (0).
- (57) Achenes six times or more longer than wide (1) or not (0).
- (58) Leaf bases cordiform (1) or not (0).
- (59) Achenes with "rostrum" (1) or not (0).
- (60) Achenes pubescent (1) or not (0).
- (61) Achenes pubescent *and* glabrous (1) or not (0).
- (62) Achenes glabrous (1) or not (0).
- (63) Style Proustia type (1) or not (0) [see text].
- (64) Style Acourtia type (1) or not (0).
- (65) Style Leucheria type (1) or not (0).
- (66) Style Onoseris stricta type (1) or not (0).
- (67) Woolly pubescence present (1) or not (0).
- (68) Receptacle with paleae in all flowers (1) or not (0).
- (69) Receptacle with paleae only in marginal flowers (1) or not (0).
- (70) Receptacle without paleae (1) or not (0).
- (71) Receptacle pubescent (1) or not (0).
- (72) Receptacle glabrous *and* pubescent (1) or not (0).
- (73) Receptacle glabrous (1) or not (0).
- (74) Habit of herbs (1) or not (0).
- (75) Habit of shrubs (1) or not (0).
- (76) Habit of vines (1) or not (0).
- (77) Capitula with 2 to 5 flowers (1) or not (0).
- (78) Capitula with 6 to 14 flowers (1) or not (0).
- (79) Capitula with 15 to 178 flowers (1) or not (0).
- (80) Corollas pubescent (1) or not (0).
- (81) Corollas 5-partite (1) or not (0).
- (82) Corollas bilabiate (1) or not (0).
- (83) Corollas bilabiate *and* 5-partite (1) or not (0).
- (84) Corollas blue (1) or not (0).

- (85) Corollas yellow (1) or not (0).
- (86) Corollas orange (1) or not (0).
- (87) Corollas red (1) or not (0).
- (88) Corollas white (1) or not (0).
- (89) Corollas violet (1) or not (0).
- (90) Anthers pubescent (1) or not (0).

Doubtless there will be slight distortion in the product resulting from the comparison of genera with different numbers of species, since the genera with the greater numbers of species may (but not always) have greater possibilities of producing more character states than those with fewer species. The project might have been more objective if the genera had the same number of species, but it is not likely that the result would have been seriously affected.

Data Processing. Given a basic data matrix (BDM) of 90 character states by 26 OTU's, the data were analyzed by three methods of numerical taxonomy. The aim of the use of more than one method is to minimize the defects of the technique. The various schemes produced can be compared in the search for common features. If such common features are found their validity is enhanced since they seem independent of the method used.

An eclectic approach was already used by Solbrig (1969) in the genus *Gutierrezia* (Compositae). As in every study based on methods of numerical taxonomy, each method included the following steps:

- 1) The obtaining of a similarity coefficient ("distance" between each pair of the 26 OTU's), this from a BDM.
- 2) The linking together (clustering) of the OTU's in a two-dimensional graph on the basis of the similarity coefficients obtained in (1).

METHOD 1. The similarity coefficient $D(A, B)$ used here is the sum, over all character states, of the absolute values of the differences between the character states in OTU A and OTU B. In the case where $X(A, i)$ denotes the character state "i" for OTU A,

$$D(A, B) = \sum |X(A, i) - X(B, i)|.$$

The resulting OTU \times OTU "distance table" (an $n \times n$ taxa matrix), TABLE 3, which gives the distance between all taxa, served as input in the calculation of a "Prim network." The Prim network technique was developed by R. C. Prim (1957) in order to determine the shortest possible network of direct links between a given set of telephone terminals. His technique can be applied as well to problems in systematic biology (Edwards & Cavalli-Sforza, 1964; Solbrig, 1969). Basically the procedure consists of choosing the shortest links connecting any two OTU's, and then by a process of elimination adding more links until all OTU's are connected in a network. This allows the construction of a two-dimensional graph representing the possible taxonomic structure.

METHOD 2. The similarity coefficient used in this method is the "distance

measure" defined by Rogers and Tanimoto (1960). This quantity $D(A, B)$ is the negative logarithm to the base 2, of the ratio of the number of character states possessed in common by OTU's A and B to the number of distinct character states possessed by A and B.

$$D(A, B) = -\log_2 \frac{\text{Character states in common in A and B}}{\text{Distinct character states possessed by A and B}}$$

The resulting OTU \times OTU "distance table" (TABLE 4) served as input to the clustering algorithm developed by Van Rijsbergen. This algorithm operates on a similarity coefficient to generate the clusters of the numerically stratified hierarchy (phenogram) specified by the single-link method. The clusters are generated level by level, starting at the lowest, so that the algorithm is of the agglomerative type. The detailed instructions for doing this are given by Van Rijsbergen (1970).

METHOD 3. The "distance table" (TABLE 3) obtained in method 1 was used as input to the clustering algorithm of Van Rijsbergen used in method 2.

TAXONOMIC HISTORY

In 1756 Patrick Browne described the genus *Trixis* in his *The Civil and Natural History of Jamaica* However, Browne did not use binomials in the first edition of his work, and in 1766 Crantz named Browne's plant *Trixis inula*. This was the first genus and the first species described in the subtribe Nassauviinae.

Several other genera were described during the next fifty years; *Jungia* Linn. f. (1781), *Nassauvia* Comm. ex Juss. (1789), *Trinacte* Gaertn. (1791), *Moscharia* Ruiz & Pavon (1794), *Triptilion* Ruiz & Pavon (1794), and *Rhinactina* Willd. (1807).

In 1811, Lagasca grouped several genera into his order "Chaenanthophorae." This order included three "sections"; the first section included those genera which are the nucleus of the subtribe Nassauviinae. The presence of only bilabiate corollas and tailed anther appendages were the diagnostic characters for his first section, which contained fourteen genera, including ten new ones, divided into two groups, those with the receptacle glabrous and those with the receptacle pubescent. Of these genera, ten are recognized today; the other four are treated as synonyms of some of these.

In 1812, Alphonse de Candolle published a paper which dealt with a new assemblage of ligulate Compositae, the Labiatiflorae. This paper was the result of research parallel with Lagasca's work on the Chaenanthophorae. The interesting history of these two parallel works has been described by Bacigalupi (1931) and by B. S. Vuilleumier (1969).

In 1817 Henri Cassini divided the "Chaenanthophorae" (or "Labiatiflorae") into two tribes on the basis of the shape of the style. His first tribe is the Mutisiées, with the stylar branch tips rounded (corresponding to sections 2 and 3 of Lagasca's Chaenanthophorae). The second tribe with

stylar branch tips truncate is the Nassauviées. This was the first use of the name, but it was not until 1819 that Cassini formally circumscribed the group as a tribe. Cassini, as did Lagasca, considered the bilabiate corollas and the tailed anthers to be important tribal characters, but he thought the truncate stylar branches were the single most unifying character. Cassini's circumscription is essentially that which is recognized today, although at the level of subtribe.

In 1825 Cassini divided the "Nassauvieae" into three sections. The first section, containing the genera *Trixis*, *Leucheria*, *Perezia*, *Jungia*, and *Panphalea*, was the most "ancient" because it showed similarities with the Senecioneae, presumably for Cassini an "ancient" group. The remaining genera, *Nassauvia*, *Triptilion*, *Polyachyrus*, *Triachne*, *Mastigophorus*, *Caloptilium*, and *Panargyrus*, were placed into a second section which Cassini considered more "specialized" than the first. The third section contained those genera which Cassini regarded as doubtful. He excluded *Proustia*, placed in this group by Lagasca, from the Nassauviées because of its rounded stylar branches.

Lessing (1830) divided the tribe "Nassauvieae" of Cassini into two subtribes, Nassauvieae and Trixideae, and here for the first time the name Nassauviinae was used at the level of subtribe (Solbrig, 1963). Bentham and Hooker (1873) retained Cassini's circumscription at the subtribal level, placing the Nassauviinae in the tribe Mutisieae. This work established the generic composition of the subtribe Nassauviinae (as well as that of the entire family) which is still used today with but minor variations. Their most important conclusions were that *Nassauvia* is closely allied to *Triptilion*; *Proustia*, which they reassigned to the Nassauviinae, is closest to *Perezia*; the genus *Cleanthes* (= *Holocheilus*) is a synonym of *Trixis*.

Hoffmann (1893) followed the classification of Bentham and Hooker, but like Cassini excluded *Proustia* and *Macrachaenium* from the Nassauviinae solely on the basis of their stylar branch tips. He did recognize *Cleanthes* as a genus distinct from *Trixis*.

Modern attempts to assess the systematics of the subtribe Nassauviinae have been made by Wodehouse (1929) on the basis of pollen morphology, by Jeffrey (1967), and by B. S. Vuilleumier (1969), each of these a preliminary survey of the group.

NOMENCLATURE

The list which follows is comprised of names that have been included in the Nassauviinae, with an indication of their present status. Those names printed in large and small CAPITALS are accepted in this paper. Names printed in *italics* are considered synonyms of accepted genera as indicated.

<i>Acanthophyllum</i> H. & A. = NASSAUVIA	<i>Caloptilium</i> Lagasca = NASSAUVIA
ACOURTIA D. Don	CALOPAPPUS Meyen
AMEGHINOIA Spegazzini	<i>Castra</i> Vellozo = HOLOCHEILUS; TRIXIS (pro parte)
<i>Bowmania</i> Gardner = TRIXIS	CEPHALOPAPPUS Nees & Martius
<i>Bridgesia</i> Hooker = POLYACHYRUS	<i>Clarionea</i> Lagasca ex DC. = PEREZIA

- Clarionea* Cassini = PEREZIA
Clarionema Philippi = PEREZIA
Cleanthes D. Don = HOLOCHEILUS
Clybatis Philippi = LEUCHERIA
Chabraea DC. = LEUCHERIA

Diaphoranthus Meyen = POLY-
ACHYRUS
DOLICHLASIUM Lagasca
Drozia Cassini = PEREZIA
Dumerilia Lagasca ex DC. = JUNGIA
Dumerilia Lessing = PEREZIA

Elizaguirrea Romy = LEUCHERIA

Gastrocarpha D. Don = MOSCHARIA

Heteranthus Cassini = PEREZIA
HOLOCHEILUS Cassini
Homanthis HBK. = PEREZIA
Homoianthus DC. = PEREZIA

JUNGIA Linnaeus f.

LEUCHERIA Lagasca
Lasiorrhiza Lagasca = LEUCHERIA
LEUNISIA Philippi
LOPHOPAPPUS Rusby

MACRACHAENIUM Hooker f.
MARTICORENIA Crisci
Martrasia Lagasca = JUNGIA
Martrasia Cassini = JUNGIA
Mastigophorus Cassini = NASSAUVIA
Mimela Philippi = LEUCHERIA

MOSCHARIA Ruiz & Pavon
Moschifera Molina = MOSCHARIA
Mosigia Sprengel = MOSCHARIA

NASSAUVIA Commerson ex Jussieu

OXYPHYLLUM Philippi

Panargyrum D. Don = NASSAUVIA
Panargyrus Lagasca = NASSAUVIA
PANPHALEA Lagasca
Pentanthus Lessing [non H. & A.; non
Raf.] = NASSAUVIA
PEREZIA Lagasca
Perezia DC. = PEREZIA Lagasca
Platycheilus Cassini = HOLOCHEILUS
PLEOCARPHUS D. Don
POLYACHYRUS Lagasca
Portalesia Meyen = NASSAUVIA
Prionanthes Schnark = TRIXIS
PROUSTIA Lagasca
Ptilurus D. Don = LEUCHERIA

Rhinactina Willd. = JUNGIA

Sphaerocephalus Lagasca ex DC. =
NASSAUVIA
Strongyloma DC. = NASSAUVIA

Tenorea Colla = TRIXIS
Triachne Cassini = NASSAUVIA
Trianthus Hooker = NASSAUVIA
Trinacte Gaertner = JUNGIA
TRIPTILION Ruiz & Pavon
TRIXIS Browne

OTHER NAMES THAT HAVE BEEN INCLUDED IN THE NASSAUVIINAE

Bertolonia DC. ex Cassini, Opus. Phyt. 2: 153. 1826. A name attributed to De Candolle by Cassini and considered a synonym of *Lasiorrhiza* Lag. In Ann. Mus. Paris 19: 65, 71. Pl. 5 (Tab. XIV). 1812, De Candolle described the new genus *Chabraea* and made the combination *Chabraea purpurea* based on *Perdicium purpureum* Vahl. He referred to Tab. XIV on the facing page (from 71), an illustration labeled *Bertolonia purpurea*, a name which does not occur anywhere else in that paper.

Cassiopea D. Don, Trans. Linn. Soc. I. 16: 215. 1830. This name is frequently listed as a synonym of *Leucheria*, but it was actually used only as a sectional name by Don and by De Candolle.

Clariona Sprengel, Linn. Syst. Veg. ed. 16. 3: 504. 1826. An orthographic variant of *Clarionea* Lag. ex DC.

Clarionia D. Don, Trans. Linn. Soc. I. 16: 204. 1830. An orthographic variant of *Clarionea* Lag. ex DC.

Frageria Delile ex Steudel, Nomencl. ed. 2. 1: 645. 1840. A nomen nudum attributed to Delile by Steudel who considered it a synonym of *Lasiorrhiza* Lag.

Homoeanthus Sprengel, Linn. Syst. Veg. ed. 16. 3: 503. 1826. An orthographic variant of *Homoianthus* Bonpl. ex DC. Ann. Mus. Paris 19: 65.

Isanthus DC. Prodr. 7: 63. 1838. An invalid name listed in the synonymy of *Homoianthus* by De Candolle.

Maclovia DC. ex Steudel, Nomencl. ed. 2. 1: 338. 1840. Listed in the synonymy of *Chabraea* DC. by Steudel, but published by De Candolle only as a section of *Chabraea*.

Microspermum Lag. Gen. Sp. Nov. 25. 1816. Although this genus has been included in the Nassauvinae by several authors, it is a member of the Helenieae.

Moscaria Persoon, Synopsis Plantarum 2: 379. 1807. An orthographic variant of *Moscharia* Ruiz & Pavon.

Pentanthus H. & A., Hooker, Comp. Bot. Mag. 1: 32. 1835 (non Lessing, nec Raf.). This taxon was cited by De Candolle as a member of the Nassauvieae, but is, rather, a member of the Senecioneae and at present is considered a synonym of *Paracalia* Cuatrecasas.

Perezia LaLlave & Lexarza ex DC. Prodr. 7: 65. 1838. A name listed by De Candolle as a synonym of *Acourtia* D. Don.

Pogonura DC. ex Lindley, Introd. Nat. Syst. ed. 2. 263. 1836. A nomen nudum attributed to De Candolle by Lindley but apparently never published by De Candolle. Frequently listed as a synonym of *Perezia* Lagasca.

Scolymanthus Willd. ex DC. Prodr. 7: 63. 1838. An invalidly published name listed by De Candolle only in the synonymy of *Homoianthus* DC.

Leukeria Endl. Enchiridion 249. 1841. An orthographic variant for *Leucheria* Lagasca.

Leuceria is an orthographic variant of *Leucheria* Lagasca which has been used rather consistently since 1830 when D. Don first took it up. In addition to Lagasca's original description (1811) and Don's paper of 1830, De Candolle in 1812 published a description of the genus using another orthographic variant, *Leucaeria*, and Lessing in 1830 called it *Leuchaeria*. There is no provision in the Code for changing Lagasca's original spelling of the name.

Anargyrum Steudel, Nomencl. ed. 2. 1: 84. 1840. A nomen nudum attributed to De Candolle by Steudel and considered a synonym of *Nassauvia*. It was published by De Candolle (Prodr. 7: 54) in a subgeneric category of *Panargyrum*.

Nassovia Batsch, Tab. Affin. Reg. Veg. 251. 1802. An orthographic variant of *Nassauvia* Comm. ex Jussieu.

Piptostemma Spach, Hist. Veg. Phan. 10: 34. 1841. A nomen nudum attributed to D. Don by Spach and considered a synonym of *Nassauvia*, but apparently never published.

RESULTS

The tribe Mutisieae is represented in both hemispheres, but most of the genera occur in the Southern Hemisphere with a great center of concentration in the southern part of the Andes of South America. Centers of lesser importance are in Mexico, in the mountains of China, and in tropical and southern Africa. In Europe there occurs only one genus, *Berardia*, its position in the Mutisieae doubtful since it presents combinations of the usual characters of the Mutisieae and of the Cynareae. The tribe Mutisieae includes about 86 genera and nearly 1000 species; these have been divided by various authors into 3 to 5 subtribes — Bentham & Hooker (1873), Barnadesieae, Onoserideae, Gochnatieae, Gerbereae, and Nassauvieae; Hoffmann (1893), Gochnatinae, Gerberinae or Mutisinae, and Nassauvinae; Cabrera (1961), Barnadesinae, Gochnatinae, Mutisinae, and Nassauvinae.

The subtribe Nassauviinae is an American group, with most genera occurring in the extratropical parts of South America. The greatest concentration of genera and of species is in the southern Andes. With the exception of *Trixis*, *Acourtia*, and *Jungia*, all of the genera of the Nassauviinae are endemic to South America. The subtribe includes about 300 species and 40 per cent of the included genera are monotypic.

Distribution and ecological conditions. Genera of the Nassauviinae occur in extratropical South America (very few in tropical parts of the continent), in Central America, in the West Indies, and in North America south of the 32nd parallel. This general area can be divided into five regions.

REGION 1: Andes of South America, north Chilean deserts, and Patagonia. Seventy per cent of the genera and species are endemic to this region. Here occur *Nassauvia*, *Triptilion*, *Leucheria*, *Moscharia*, *Oxyphyllum*, *Polyachyrus*, *Marticorenia*, *Leunisia*, *Macrachaenium*, *Pleocarphus*, *Ameghinoa*, *Dolichlasium*, *Lophopappus*, *Proustia*, *Calopappus*, and one of the critical taxa, *Perezia lanigera*. Although *Jungia*, *Trixis*, and *Perezia* are not endemic to this region, they do occur here, and most of the species of *Perezia* occur in the Andes.

Several major kinds of vegetation, each occupying numerous microhabitats, occur in the Andes, and in each of these microhabitats there are found some species of Nassauviinae. Most of this region is dry and/or at high altitudes, but it does include some moist environments, such as the páramos of Venezuela, Colombia, and Ecuador, where a few species of *Perezia* occur, and, in the south, the *Nothofagus* forest, where there occur a few species of *Perezia* and of *Leucheria* and *Macrachaenium*, which is endemic to the forest. This region is topographically young, for the final Andean uplift occurred only in the Tertiary.

REGION 2: Southern Brazil, Paraguay, Uruguay, and northeastern Argentina. Here occur *Panphalea*, *Holocheilus*, *Trixis*, *Jungia*, *Perezia*, and one of the critical taxa, *Onoseris stricta*. This is a region of plains and low mountains, with a temperate and moist climate.

REGION 3: Tropical South America. There are very few species and genera of Nassauviinae in this region; those that do occur are sparsely distributed. The monotypic genus, *Cephalopappus*, endemic to the state of Bahia in Brazil, occurs in this region as do also a few species of *Trixis* and *Jungia*. The climate is warm and moist.

REGION 4: Central America, Mexico, and the United States (south of the 32nd parallel). Here there occur *Acourtia*, *Trixis*, a few species of *Jungia*, and one of the critical taxa, *Gochnatia glomeriflora*. The climate is relatively warm.

REGION 5: West Indies. In this region occur only two species of *Trixis*, *T. inula* and *T. divaricata*, and one of the critical taxa, *Proustia vanillosma*. The climate where these plants are found is warm and semiarid.

Since most of the species occur in regions which are dry and/or at high altitudes, with frequent frosts, they show many adaptations to xerophytic conditions. Some of these adaptations are reflected in the time of flowering, in habit, type of growth, and in seed germination. Some correspondences between habit and habitat were pointed out by B. S. Vuilleumier (1969: 20) for the genus *Perezia*, and these observations can be generalized for the majority of species of Nassauviinae.

Morphological Analysis. A. HABIT: Comparative studies of the genera and species of Compositae indicate that the ancestral prototype probably was a woody plant, either a large shrub or a small tree (Carlquist, 1966). This assumption can be extended to the Nassauviinae in which occur three kinds of habit, herbaceous, shrubby, and scandent. We can further assume that the herbs and climbers have evolved from shrubby ancestors in two different lines. At the levels of both genus and species the herbaceous habit is predominant and *Perezia*, *Leucheria*, *Moscharia*, *Triptilion*, *Macrachaenium*, *Calopappus*, *Panphalea*, *Holocheilus*, *Cephalopappus*, *Polyachyrus*, and *Onoseris stricta* are all perennial or annual herbs.

Most of the species of *Nassauvia* are perennial herbs, but some are small shrubs. *Jungia* includes both shrubby and scandent species, but one, *J. stuebellii*, is herbaceous. *Acourtia* includes perennial herbs and shrubs. All of the species of *Oxyphyllum*, *Marticoenia*, *Leunisia*, *Pleocarphus*, *Ameghinoa*, *Dolichlasium*, and *Trixis* are shrubby, as is one of the critical taxa, *Gochnatia glomeriflora*. *Proustia* includes both shrubby and scandent species; one of the critical taxa, *P. vanillosma*, is scandent. *Perezia lanigera* is a caespitose shrub.

B. PAPPUS: In *Cephalopappus* and *Panphalea* the pappus is absent; species of both genera occur in similar habitats, in moist places near water courses, and if water is the agent of achene dispersal, it might be that the pappus has become functionally superfluous. In species of *Moscharia* and *Polyachyrus* the pappus is greatly reduced. In both genera the capitula are reduced and only 2-flowered, but an enlarged involucre bract surrounds the achenes and apparently plays a part in dispersal. An analogous case is that in *Madia*, a genus of Heliantheae, but at the level of the flower and paleae.

The pappus in genera of Nassauviinae is made up of hairs or paleae.

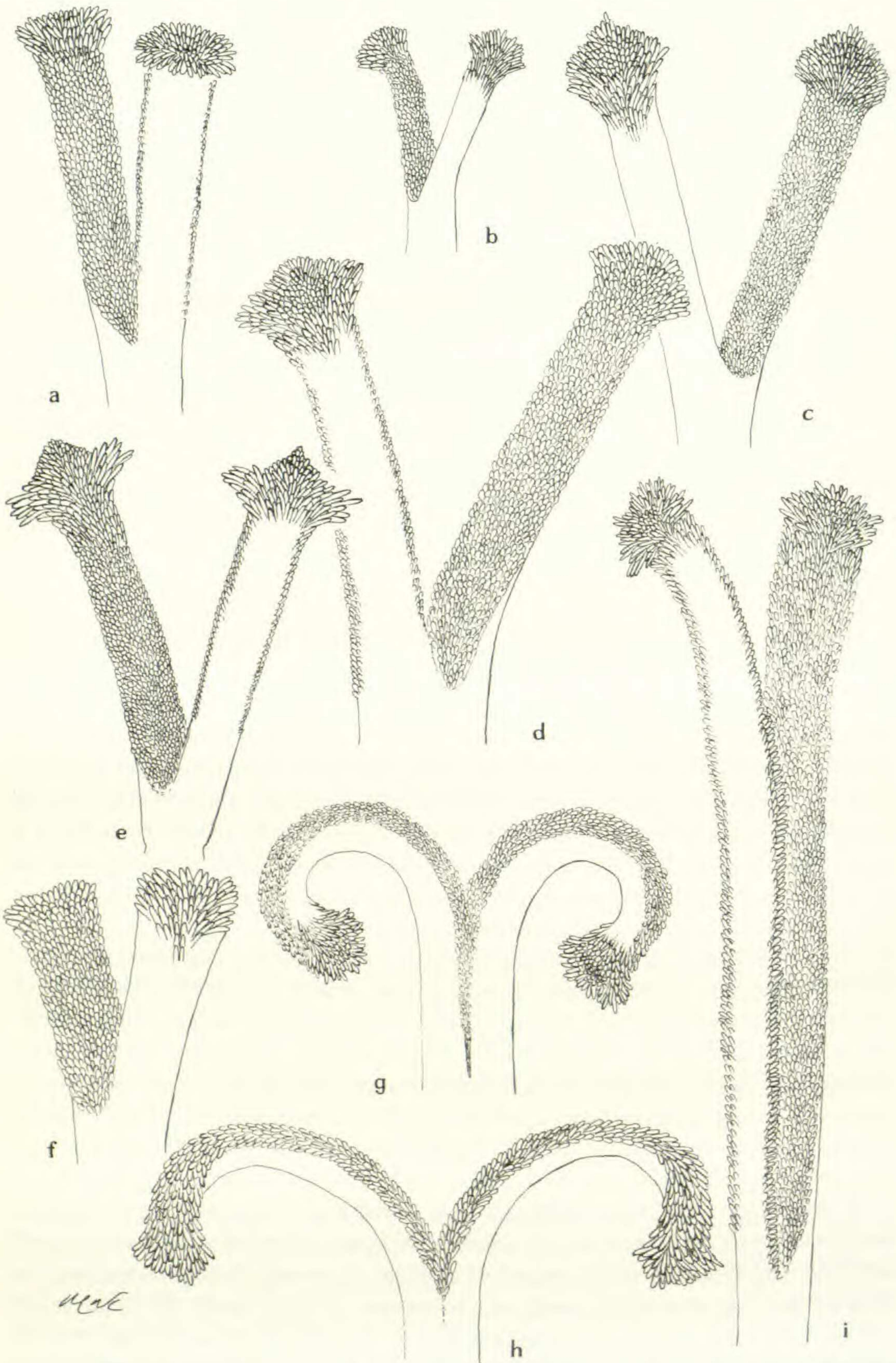


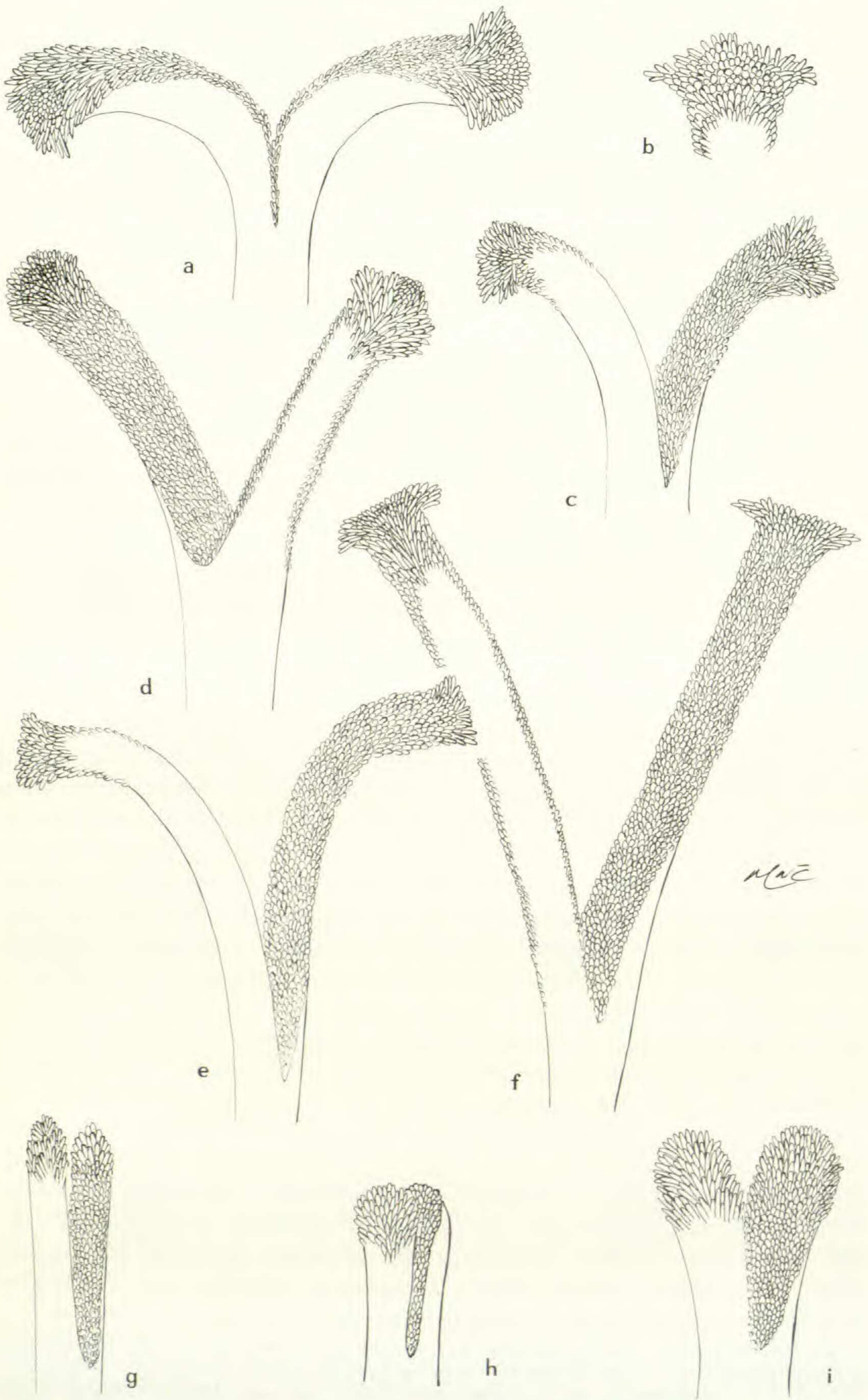
FIGURE 1. Types of styles in Nassauviinae. Truncate type: a, *Perezia magellanica*, $\times 35$ (Cunningham s.n., GH); b, *Panphalea commersonii*, $\times 35$ (Dusén 930, GH); c, *Triptilion spinosum*, $\times 35$ (Walter 230, GH); d, *Ameghinoa patagonica*, $\times 35$ (Donat 236, GH); e, *Nassauvia magellanica*, $\times 35$ (Hatcher 1897,

Chaffy pappus occurs in *Moscharia*, *Nassauvia*, *Triptilion*, and *Calopappus*. Hairy pappus can be of two kinds: setose, as in *Perezia*, *Acourtia*, *Leucheria*, *Polyachyrus*, *Leunisia*, *Pleocarphus*, *Jungia*, *Trixis*, *Ameghinoa*, *Dolichlasium*, *Holocheilus*, *Lophopappus*, *Proustia*, *Proustia vanillosma*, *Gochnatia glomeriflora*, *Onoseris stricta*, and *Perezia lanigera*, or plumose, as in *Nassauvia*, *Leucheria*, *Polyachyrus*, *Jungia*, *Oxyphyllum*, *Macrachaenium*, and *Marticoenia*. The pappus can be disposed in a single series (*Nassauvia*, *Triptilion*, *Leucheria*, *Moscharia*, *Oxyphyllum*, *Polyachyrus*, *Jungia*, *Calopappus*, *Marticoenia*) or in more than one (*Perezia*, *Acourtia*, *Leunisia*, *Macrachaenium*, *Pleocarphus*, *Trixis*, *Ameghinoa*, *Dolichlasium*, *Holocheilus*, *Lophopappus*, *Proustia*, *Proustia vanillosma*, *Gochnatia glomeriflora*, *Onoseris stricta*, *Perezia lanigera*). It can be white (*Nassauvia*, *Triptilion*, *Leucheria*, *Moscharia*, *Oxyphyllum*, *Polyachyrus*, *Leunisia*, *Macrachaenium*, *Dolichlasium*, *Holocheilus*, *Calopappus*, *Marticoenia*, *Gochnatia glomeriflora*) or colored (*Pleocarphus*, *Ameghinoa*, *Lophopappus*, *Proustia vanillosma*, *Onoseris stricta*), and there are genera such as *Perezia*, *Acourtia*, *Jungia*, *Trixis*, and *Proustia* which include both species with white and those with colored pappus.

Cronquist (1955) has pointed out that chaffy pappus is the most primitive type, but it is difficult to reconcile this assumption with the situation in the Nassauviinae, for chaffy pappus is always associated, as in the genus *Nassauvia*, with evolutionarily advanced features.

C. INFLORESCENCES: In the Nassauviinae there is a group of genera, *Triptilion*, *Nassauvia*, *Polyachyrus*, and *Moscharia*, which shows a trend toward reduction of the number of flowers in the capitula and aggregation of the capitula themselves into a capitate secondary inflorescence, as a "pseudocephalium." The occurrence of a pseudocephalium, as compared to a regular capitulum, is believed to be an evolutionarily advanced feature. In the genus *Nassauvia* are found all stages between a solitary capitulum and a pseudocephalium. Characters of the inflorescence show the following variations: capitula solitary (*Perezia*, *Acourtia*, *Leucheria*, *Leunisia*, *Macrachaenium*, *Dolichlasium*, *Holocheilus*, *Lophopappus*, *Cephalopappus*, *Calopappus*, *Onoseris stricta*, *Perezia lanigera*); spicate (*Nassauvia*); cymose or paniculate (*Perezia*, *Acourtia*, *Leucheria*, *Oxyphyllum*, *Pleocarphus*, *Jungia*, *Trixis*, *Ameghinoa*, *Panphalea*, *Holocheilus*, *Lophopappus*, *Proustia*, *Marticoenia*, *Proustia vanillosma*, *Gochnatia glomeriflora*); in a glomerulum or in a pseudocephalium (*Nassauvia*, *Triptilion*, *Moscharia*, *Polyachyrus*). Three kinds of capitula can be recognized: sessile (*Nassauvia*, *Triptilion*, *Moscharia*, *Polyachyrus*, *Calopappus*); subsessile (*Acourtia*, *Proustia*, *Proustia vanillosma*, *Gochnatia glomeriflora*, *Perezia lanigera*); and pedicellate (*Perezia*, *Leucheria*, *Oxyphyllum*, *Leunisia*, *Macrachaenium*, *Pleocarphus*, *Jungia*, *Trixis*, *Ameghinoa*, *Dolichlasium*, *Panphalea*, *Holocheilus*, *Lophopappus*, *Cephalopappus*, *Marticoenia*, *Onoseris stricta*).

D. RECEPTACLE: Receptacular bracts are not common in the Mutisieae, GH); f, *Perezia lanigera*, $\times 35$ (Ruiz Leal 26875, LP); g, *Oxyphyllum ulicinum*, $\times 35$ (Johnston 5153, GH); h, *Jungia ferruginosa*, $\times 35$ (Skutch 3622, GH); i, *Marticoenia foliosa*, $\times 35$ (Zollner 2994, LP).



occurring on only 10 per cent of the genera. When receptacular bracts do occur, they can either subtend all the flowers or be restricted to the marginal flowers. Among the genera of Nassauviinae receptacular bracts subtending all the flowers occur in species of three genera, *Jungia*, *Pleocarphus*, and *Marticoenia*. In other cases the paleae are restricted to the margin of the receptacle, as in *Oxyphyllum* and some species of *Leucheria*. In the genus *Polyachyrus* occurs a bract which can be interpreted either as an involucre bract or as a receptacular bract. Most authors, such as Cronquist (1955), who have dealt with evolution in the Compositae regard the presence of receptacular bracts as primitive.

The receptacle can be glabrous, as in *Nassauvia*, *Moscharia*, *Holocheilus*, *Calopappus*, *Polyachyrus*, *Macrachaenium*, *Ameghinoa*, *Dolichlasium*, *Panphalea*, *Holocheilus*, *Calopappus*, and *Leucheria*, or pubescent, as in *Acourtia*, *Leunisia*, *Pleocarphus*, *Jungia*, *Trixis*, *Lophopappus*, *Proustia*, *Cephalopappus*, *Marticoenia*, *Gochnatia glomeriflora*, *Onoseris stricta*, and *Perezia lanigera*. There are also genera including both species with a glabrous receptacle and species with the receptacle pubescent (*Perezia* and *Triptilion*). At present it is nearly impossible to describe evolutionary trends for this character, but when it is associated with other characters, it would seem that the pubescent receptacle is the more primitive.

E. FLOWERS: The Nassauviinae have always been described as having the corollas bilabiate with the outer lip three-toothed and the inner bifid. However, some of the taxa here considered have 5-partite corollas. Transition from one type to the other is simple; it requires only that the cleft between two of the corolla segments be deepened. Such a transition occurs also in other subtribes of Mutisieae, as in the genera *Flotovia* and *Chuquiraga*. On the other hand, complete or partial fusion of three segments of the corolla results in a bilabiate corolla. In the genus *Lophopappus* are found all stages between 5-partite and bilabiate corollas. In *L. peruvianus* all the flowers have 5-partite corollas; in *L. berberidifolius* most are 5-partite, but some are bilabiate; in *L. blakei* all the flowers have bilabiate corollas, but the outer lip is irregularly divided; in *L. cuneatus* and *L. foliosus* all flowers have the corolla bilabiate with the outer lip deeply three-toothed. In the genus *Proustia* some individuals of *P. pyrifolia* have some flowers with the corolla 5-partite in a capitulum in which most of the flowers have a bilabiate corolla. In *Acourtia collina* 5-partite corollas occur, as they do in *Gochnatia glomeriflora*, one of the critical taxa. Another critical taxon, *Onoseris stricta*, has capitula with both types of corolla, but in a radiate position.

FIGURE 2. Types of styles in Nassauviinae (continued). Truncate type: a, *Polyachyrus annuus*, $\times 35$ (Worth & Morrison 15758, GH); b, *Leucheria purpurea*, $\times 35$ (Goodall 4146, GH); c, *Holocheilus brasiliensis*, $\times 35$ (Pedersen 6122, GH); d, *Trixis inula*, $\times 35$ (Skutch 2614, GH); e, *Pleocarphus revolutus*, $\times 35$ (Zollner 475, GH); f, *Dolichlasium lagascae*, $\times 22$ (Cabrera 17942, LP). Proustia type: g, *Macrachaenium gracile*, $\times 35$ (Parodi 11739, GH); h, *Cephalopappus sonchifolius*, $\times 35$ (Martius 1816, M); i, *Lophopappus foliosus*, $\times 35$ (Buchtien 598, GH).

It is possible that the trend of evolution in this character has been from flowers 5-partite to flowers bilabiate, for the 5-partite condition occurs in genera of the subtribe Gochnatiinae which is thought to be the most primitive of the subtribes of Mutisieae. On the other hand, very advanced genera, such as *Moscharia* in which pseudocephalia occur, have flowers with bilabiate corollas. Among genera of the Nassauviinae, the number of flowers per capitulum varies from 2 to 178. As was pointed out by Stebbins (1967), the number of flowers per capitulum is more nearly constant when there are only few flowers; in many-flowered inflorescences the range of variation is greater. This generalization seems to be valid for the Nassauviinae. On the basis of this assumption the total range of variation, i.e., from 2 to 178, has been divided into three sets: 2–5, 6–14, and 15–178. There occur 2 to 5 flowers per capitulum in *Nassauvia*, *Triptilion*, *Moscharia*, *Polyachyrus*, and *Calopappus*; 6 to 14 in *Acourtia*, *Oxyphyllum*, *Trixis*, *Panphalea*, *Lophopappus*, *Proustia*, *Gochnatia glomeriflora*, and *Perezia lanigera* (in some individuals in species of these genera there very rarely occur more than 14 flowers); 15 to 178 in *Perezia*, *Leucheria*, *Leunisia*, *Jungia*, *Macrachaenium*, *Pleocarphus*, *Ameghinoa*, *Dolichlasium*, *Holocheilus*, *Cephalopappus*, *Marticoenia*, and *Onoseris stricta*. To determine the trend of evolution for this character is difficult; the character may be used for taxonomic purposes, but not to determine the evolutionary pathway.

In the Nassauviinae the corolla can be glabrous (*Perezia*, *Nassauvia*, *Triptilion*, *Leucheria*, *Oxyphyllum*, *Polyachyrus*, *Leunisia*, *Macrachaenium*, *Dolichlasium*, *Lophopappus*, *Proustia*, *Calopappus*, *Onoseris stricta*) or pubescent (*Acourtia*, *Moscharia*, *Pleocarphus*, *Jungia*, *Trixis*, *Ameghinoa*, *Panphalea*, *Holocheilus*, *Cephalopappus*, *Marticoenia*, *Proustia vanillosma*, *Gochnatia glomeriflora*, *Perezia lanigera*).

The color of the flowers can be blue (*Perezia*, *Nassauvia*, *Triptilion*, *Leucheria*), yellow (*Leunisia*, *Pleocarphus*, *Trixis*, *Ameghinoa*, *Dolichlasium*, *Calopappus*, *Proustia vanillosma*, and a few species of *Perezia* and *Jungia*), orange (*Cephalopappus* and *Onoseris stricta*), red (*Perezia*, *Polyachyrus*, *Proustia*), white (*Perezia*, *Nassauvia*, *Triptilion*, *Leucheria*, *Moscharia*, *Polyachyrus*, *Jungia*, *Panphalea*, *Holocheilus*, *Lophopappus*, *Proustia*, *Perezia lanigera*), or violaceous (*Perezia*, *Acourtia*, *Nassauvia*, *Leucheria*, *Oxyphyllum*, *Macrachaenium*, *Jungia*, *Marticoenia*). Cronquist (1955) has pointed out that yellow is the primitive stage of this character in the Compositae.

In *Leunisia*, *Dolichlasium*, and *Proustia* there occur anthers with hairs.

F. ACHENES: The achenes show a wide range of morphological variation. In genera such as *Leunisia*, *Macrachaenium*, *Pleocarphus*, *Jungia*, *Trixis*, *Dolichlasium*, and *Cephalopappus*, the achenes are 5 times longer than wide. Other genera have a rostrum, well developed in *Dolichlasium*, less so in *Leunisia*, *Macrachaenium*, *Pleocarphus*, *Jungia*, *Trixis*, and *Cephalopappus*. The achenes can be glabrous (*Macrachaenium*, *Cephalopappus*, *Calopappus*) or pubescent (*Perezia*, *Acourtia*, *Moscharia*, *Oxyphyllum*, *Leunisia*, *Pleocarphus*, *Jungia*, *Trixis*, *Ameghinoa*, *Dolichlasium*, *Panphalea*, *Holocheilus*, *Lophopappus*, *Proustia*, *Cephalopappus*, *Marticoenia*,

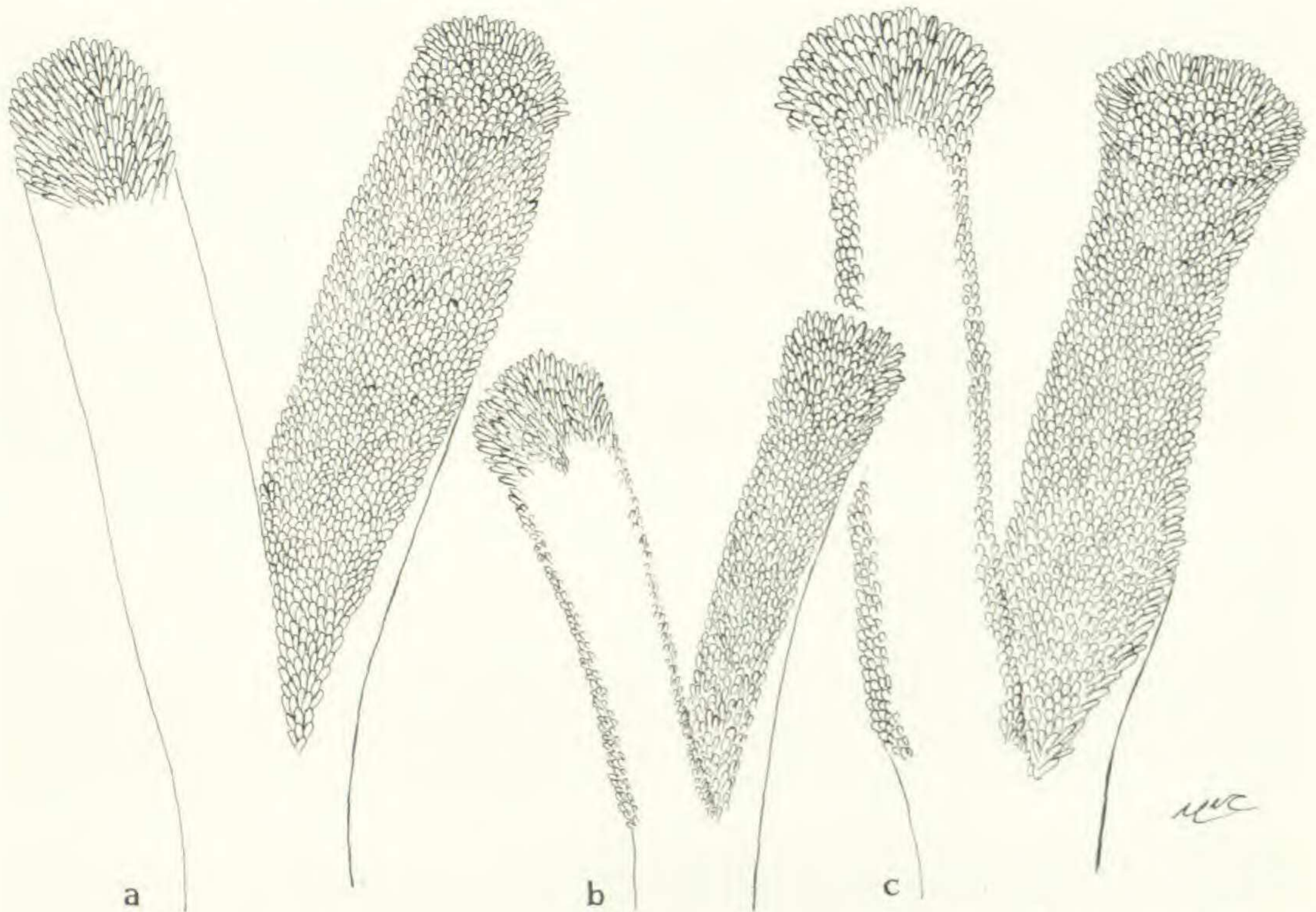


FIGURE 3. Types of styles in Nassauviinae (continued). *Acourtia* type: a, *Perezia nutans*, $\times 35$ (Vuilleumier 223, GH); b, *Acourtia glomeriflora*, $\times 35$ (Pringle 9946, GH); c, *Leunisia leata*, $\times 35$ (Morrison 17024, GH).

Proustia vanillosma, *Gochnatia glomeriflora*, *Onoseris stricta*, *Perezia lanigera*) and there are also genera including both species with glabrous achenes and species with pubescent achenes (*Nassauvia*, *Triptilion*, *Leucheria*, *Polyachyrus*).

G. TYPE OF PUBESCENCE: The commonest type of pubescence, made up of woolly trichomes, occurs in *Acourtia*, *Leucheria*, *Oxyphyllum*, *Polyachyrus*, *Macrachaenium*, *Pleocarphus*, *Jungia*, *Trixis*, *Lophopappus*, *Proustia*, *Cephalopappus*, *Proustia vanillosma*, *Onoseris stricta*, *Gochnatia glomeriflora*, and *Perezia lanigera*. There do occur other kinds of trichomes, such as glandular uniseriate, nonglandular uniseriate, and double trichomes ("Zwillingshaare"), but until trichome types have been more thoroughly studied, they cannot be used for taxonomic purposes. Stebbins's (1967: 111) observation that "The strong development of multicellular glandular trichomes is a widespread feature of xeric and semixerix species of Compositae" is valid for the Nassauviinae.

H. LEAVES: All the genera of the subtribe have alternate leaves; leaf morphology is very useful for the separation of species, but much less so for the delimitation of genera. It is, however, possible to point out some features. *Jungia* has orbicular cordate leaves (except *J. stuebelii*). In both *Trixis* and *Pleocarphus* the blades are several times (at least five) longer than wide. In *Marticoenia* all leaves are sessile. In some genera all the species have entire leaves (*Acourtia*, *Nassauvia*, *Leunisia*, *Pleocarphus*, *Jungia*, *Trixis*, *Lophopappus*, *Proustia*, *Cephalopappus*, *Calopappus*, *Marti-*

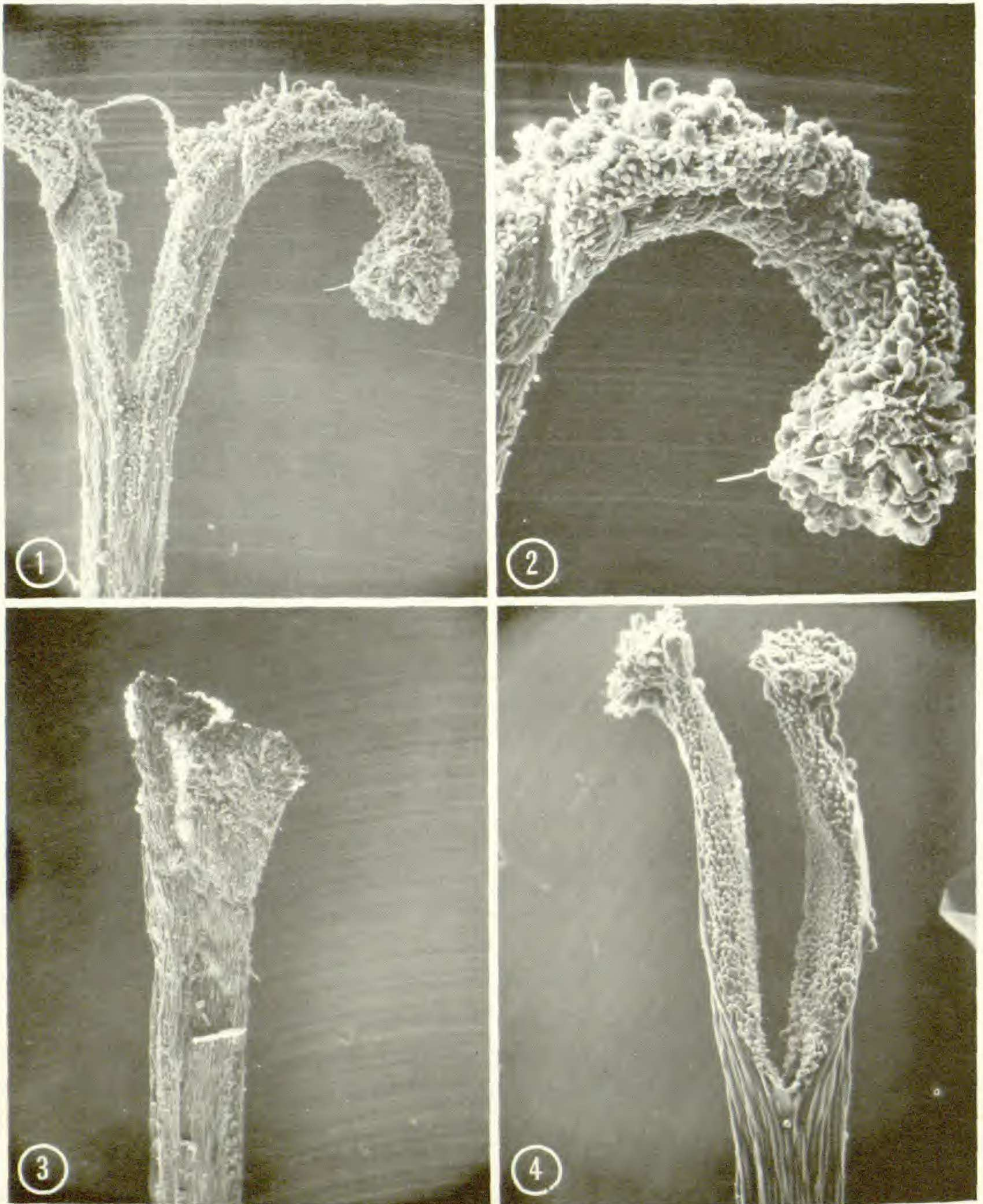


FIGURE 4. Types of styles in Nassauviinae (continued). Scanning electron micrographs (SEMG). Truncate type: 1 and 2, *Jungia ferruginosa*, $\times 65$ and $\times 130$ (Skutch 3622, GH); 3, *Calopappus acerosus*, $\times 33$ (Wederman 638, GH); 4, *Leucheria purpurea*, $\times 65$ (Goodall 4146, GH).

corenia, *Proustia vanillosma*, *Gochnatia glomeriflora*, *Onoseris stricta*, *Perezia lanigera*); in other genera all the species have partite leaves (*Triptilion*, *Moscharia*, *Oxyphyllum*, *Polyachyrus*, *Macrachaenium*, *Ameghinoa*, *Dolichlasium*) and there are genera including species with entire leaves and species with partite leaves (*Perezia*, *Leucheria*, *Panphalea*, *Holocheilus*).

In *Nassauvia*, *Triptilion*, *Oxyphyllum*, *Calopappus*, and *Perezia lanigera*

all species have leaves with a spiny margin; this character occurs also in *Perezia*, *Acourtia*, *Lophopappus*, and *Proustia*, but not in all species.

I. STYLE: The Nassauviinae have always been described as having the styles bifid, the branches flattened and truncate, glabrous on the outer surface, crowned with elongate collecting hairs at the apices and papillose with shorter ones on the adaxial surfaces. However, a careful study of styles in the taxa dealt with here shows that there occur four basic types. In every genus except *Perezia* the styler type is uniform among all the species.

The first type has truncate styler branches (*Perezia*, *Nassauvia*, *Tripti-*

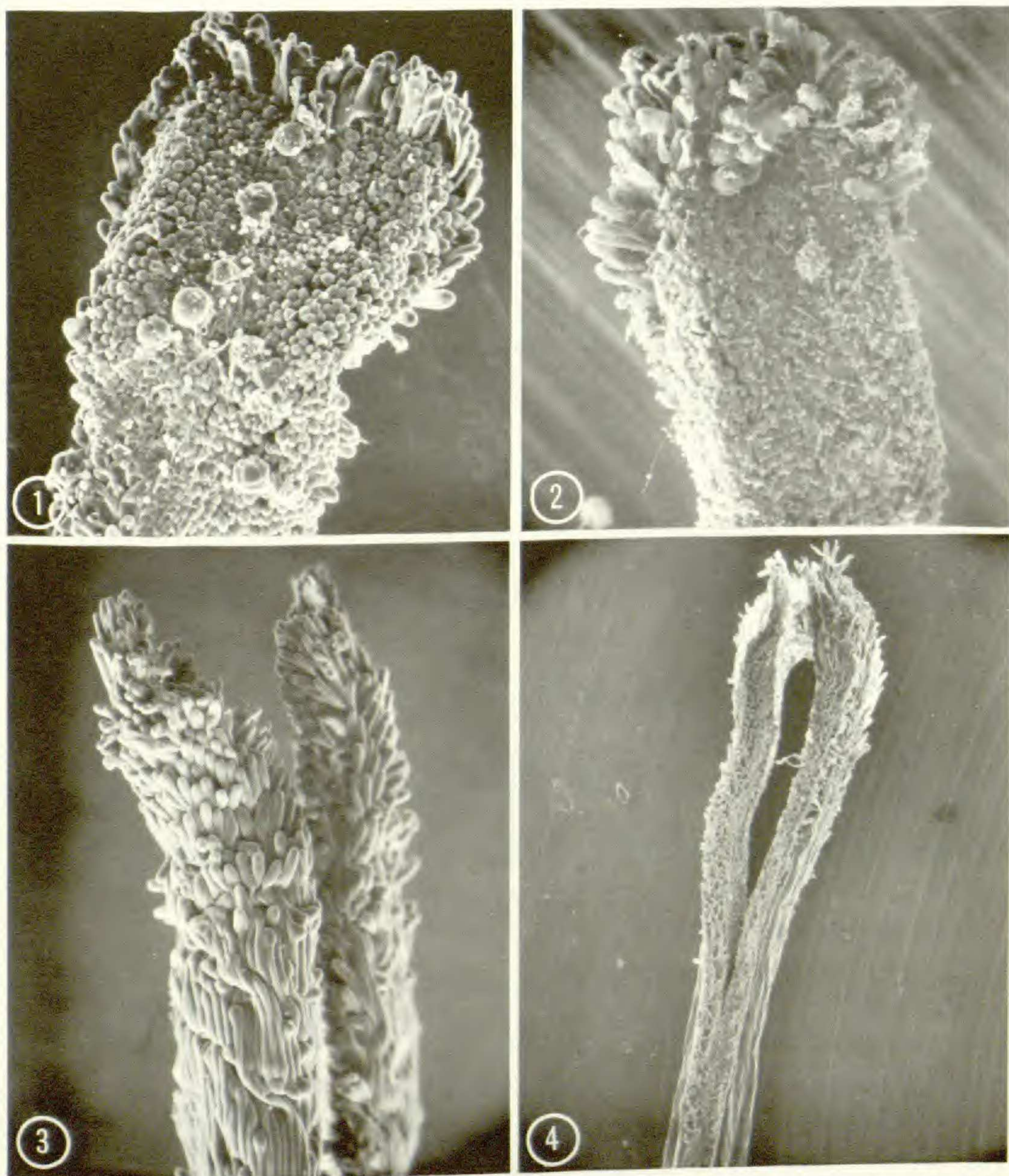


FIGURE 5. Types of styles in Nassauviinae (continued). Scanning electron micrographs (SEMG). *Acourtia* type: 1, *Acourtia reticulata*, $\times 130$, stigma (*Bourgeau 3096*, GH); 2, *Acourtia vanillosma*, $\times 130$ (*Otero 391*, GH). *Proustia* type: 3, *Proustia pyrifolia*, $\times 130$ (*Morrison 17163*, GH). *Onoseris stricta* type: 4, *Onoseris stricta*, $\times 33$ (*Ibarrola 1174*, GH).

lion, *Leucheria*, *Moscharia*, *Oxyphyllum*, *Polyachyrus*, *Pleocarphus*, *Jungia*, *Trixis*, *Ameghinoa*, *Dolichlasium*, *Holocheilus*, *Calopappus*, *Marticoenia*, and *Perezia lanigera*). The second (*Proustia*) type has the branches less than 1 mm. long, rounded at the apex, bearing long papillae on the distal half of the outer surface, but completely papillose on the inner surface (*Macrachaenium*, *Lophopappus*, *Proustia*, *Cephalopappus*). The third (*Acourtia*) type has the branches more than 1 mm. long with the apices rounded and slightly expanded. The outer surfaces bear long papillae on the distal fifth; the inner surfaces are completely papillose. This type occurs in *Acourtia*, *Leunisia*, *Proustia vanillosma*, *Gochnatia glomeriflora*, and in two species of *Perezia*, *P. nutans* and *P. prenanthoides*. The fourth type occurs only in *Onoseris stricta*. The stylar branches are spatulate. The inner surfaces are completely covered with short papillae, and the distal third of the outer surfaces bears very long papillae. FIGURES 1 to 5 show the different types of styles found in Nassauviinae.

J. POLLEN: Pollen characteristics have been very useful in delimiting genera of the Nassauviinae, but much less so for separating species. Wodehouse (1929), Stix (1960), Skvarla and Turner (1966), Crisci (1971a and b), and Parra and Marticoenia (1972) have contributed to our knowledge of pollens in the Nassauviinae. In this study the following characters have been used: grain shape, exine morphology, presence or absence of polar elevations, presence or absence of sexine processes.

On the basis of shape, pollen grains of the Nassauviinae can be divided into four types (the fractions refer to the relation between polar axis and equatorial axis): oblate-spheroidal (7/7–8/8) (*Perezia*, *Nassauvia*, *Triptilion*, *Leucheria*, *Cephalopappus*, *Calopappus*, *Perezia lanigera*); prolate-spheroidal (8/8–8/7) (*Perezia*, *Acourtia*, *Nassauvia*, *Triptilion*, *Leucheria*, *Moscharia*, *Oxyphyllum*, *Polyachyrus*, *Jungia*, *Panphalea*, *Holocheilus*, *Lophopappus*, *Proustia*, *Cephalopappus*, *Calopappus*, *Marticoenia*, *Proustia vanillosma*, *Gochnatia glomeriflora*, *Perezia lanigera*); subprolate (8/7–8/6) (*Perezia*, *Acourtia*, *Leucheria*, *Oxyphyllum*, *Polyachyrus*, *Macrachaenium*, *Pleocarphus*, *Jungia*, *Holocheilus*, *Lophopappus*, *Proustia*, *Marticoenia*, *Proustia vanillosma*, *Gochnatia glomeriflora*); prolate (8/6–8/4) (*Leucheria*, *Oxyphyllum*, *Leunisia*, *Macrachaenium*, *Pleocarphus*, *Trixis*, *Ameghinoa*, *Dolichlasium*, *Proustia*, *Onoseris stricta*).

As is shown, some taxa include more than one type. Sexine processes are structures found on the membrane of the colpus in the pollen of some taxa (*Perezia*, *Acourtia*, *Nassauvia*, *Triptilion*, *Leunisia*, *Jungia*, *Trixis*, *Ameghinoa*, *Dolichlasium*, *Panphalea*, *Holocheilus*, *Lophopappus*, *Proustia*, *Cephalopappus*, *Calopappus*, *Proustia vanillosma*, *Gochnatia glomeriflora*, *Onoseris stricta*, *Perezia lanigera*). They are more or less spherical and seem to be connected to the membrane by short thin pedicels.

In some genera (*Perezia*, *Leucheria*, *Holocheilus*, and *Proustia*) the pollen grains have polar elevations; these are extremely well developed in *Oxyphyllum*, *Leunisia*, *Trixis*, *Ameghinoa*, *Dolichlasium*, and in *Onoseris stricta*.

Morphology of the exine is a very useful character in the systematics of the genera of Compositae. Stix has pointed out that in Compositae there occur 42 types of exine stratification. Five types of exine are found in the Nassauviinae; two were pointed out by Stix, two by Parra and Marticorena, and the last (*Cephalopappus*) type is from unpublished data kindly provided by C. Marticorena.

Oxyphyllum type: The tectum and infratectum are of the same thickness and are separated from each other by a thin layer not parallel to the nexine (zigzag). It occurs in two subtypes: (a) the tectum with short ramifications (bacules) near the terminal membrane (*Perezia*, *Moscharia*, *Oxyphyllum*, *Panphalea*) and (b) the tectum lacking ramification (*Nassauvia*, *Triptilion*, *Leucheria*, *Polyachyrus*).

Trixis type: The tectum and infratectum are of different thicknesses and are separated from each other by a thick layer parallel to the nexine. This type is found in *Acourtia*, *Leunisia*, *Macrachaenium*, *Pleocarphus*, *Jungia*, *Trixis*, *Ameghinoa*, *Dolichlasium*, *Holocheilus*, *Marticorenia*, *Proustia vanillosma*, *Gochnatia glomeriflora*, *Onoseris stricta*, and *Perezia lanigera*. Stix recognized in this group two types, the Trixis type and the Ameghinoa type, on the basis of the presence of vestiges of spines, but this is a feature seen in all genera of the group.

Proustia type: The tectum and infratectum are of equal thickness and are separated from each other by a thick layer almost parallel to the nexine. This type occurs in *Proustia* and in *Lophopappus*. There is here a tendency toward the Trixis type.

Calopappus type: (= *Nassauvia remyana* type of Parra & Marticorena, 1972). The infratectum is thicker than the tectum. The tectum and infra-

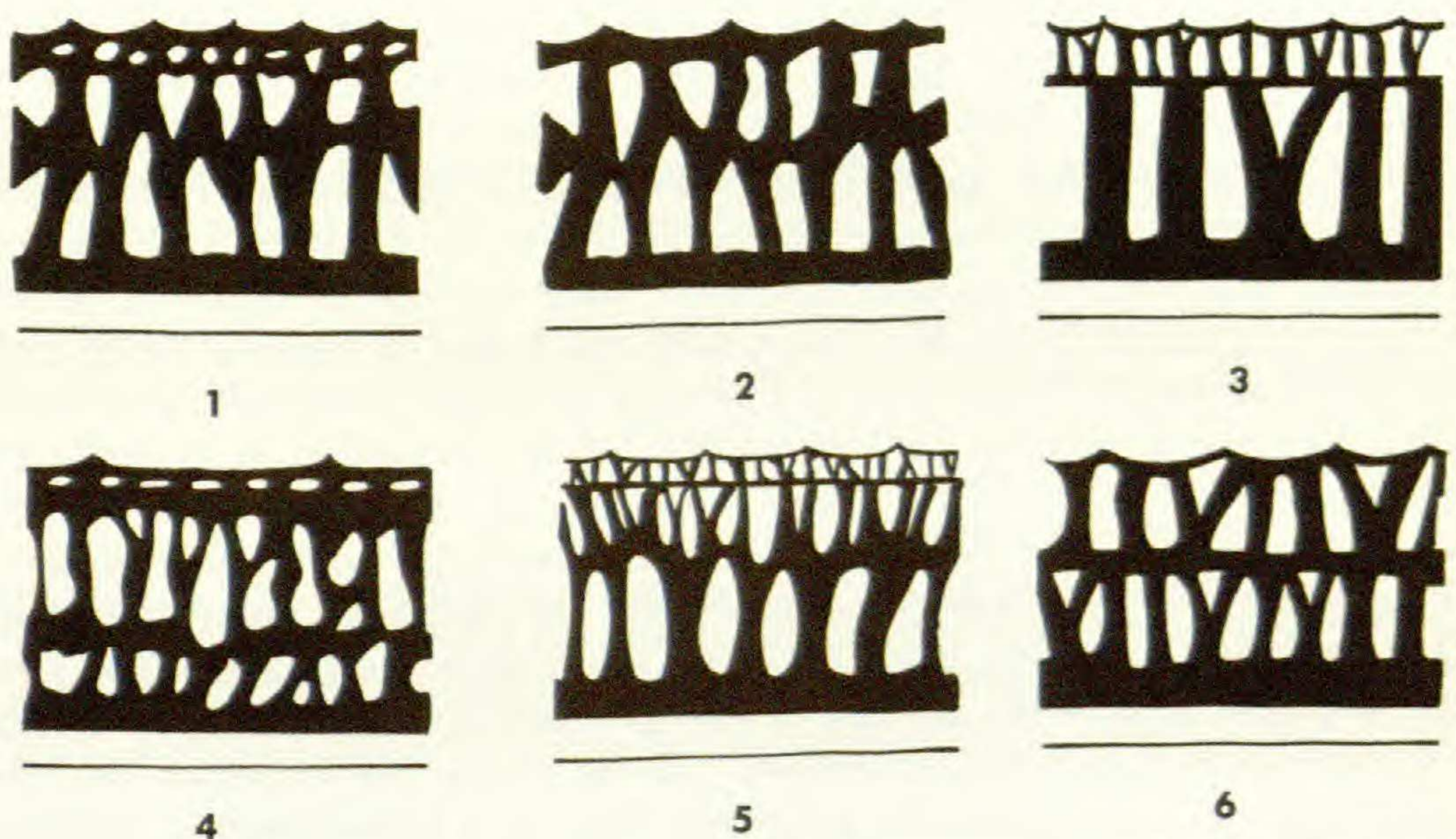


FIGURE 6. Types of exine stratification in Nassauviinae in a simplified form (see text): 1, Oxyphyllum (a) type; 2, Oxyphyllum (b) type; 3, Trixis type; 4, Cephalopappus type; 5, Calopappus type; 6, Proustia type.

teetum are separated from each other by a thick layer not parallel to the nexine (zigzag). This type occurs in *Calopappus*.

Cephalopappus type: The teetum has short ramifications and is thicker than the infrateetum. The teetum and infrateetum are separated by a thick layer parallel to the nexine. This type occurs in *Cephalopappus*.

In FIGURE 6 are shown in a simplified form the types of exine stratification in Nassauviinae.

Wodehouse (1929) pointed out that the Nassauviinae may represent the culmination of three more or less distinct developmental trends in pollen morphology; i.e., toward reduction of spines, toward lengthening of the furrows, and toward elliptical grains. On the basis of pollen morphology Wodehouse concluded that the various genera of the Nassauviinae seem to be closely related, and to represent the end of a phylogenetic line within the tribe Mutisieae. Wodehouse's conclusion seems to be correct, but some characters, such as elliptical grains, are found associated with other features thought to be primitive. At present characters of the pollen seem to be very useful in the systematics of the group, but are not so helpful in determining phylogenetic relationships within the group.

K. INVOLUCRE: The involucre offers numerous characters useful in the systematics of the subtribe.

Four involucre shapes occur: (1) campanulate (*Acourtia*, *Leucheria*, *Leunisia*, *Macrachaenium*, *Dolichlasium*, *Lophopappus*, *Jungia*, *Trixis*, *Perezia lanigera*); (2) hemispherical (*Perezia*, *Leucheria*, *Pleocarphus*, *Ameghinoa*, *Panphalea*, *Holocheilus*, *Cephalopappus*, *Marticoenia*, *Onoseris stricta*); (3) cylindrical (*Perezia*, *Acourtia*, *Nassauvia*, *Triptilion*, *Oxyphyllum*, *Polyachyrus*, *Jungia*, *Trixis*, *Lophopappus*, *Proustia*, *Calopappus*, *Proustia vanillosma*, *Gochnatia glomeriflora*); (4) turbinate (*Perezia*, *Acourtia*, *Leucheria*, *Jungia*). There can be one or two rows of involucral bracts (as in *Nassauvia*, *Triptilion*, *Moscharia*, *Polyachyrus*, *Leunisia*, *Pleocarphus*, *Jungia*, *Trixis*, *Ameghinoa*, *Macrachaenium*, *Dolichlasium*, *Panphalea*, *Holocheilus*, and *Marticoenia*) or three or more (as in the genera *Acourtia*, *Oxyphyllum*, *Lophopappus*, *Proustia*, *Cephalopappus*, *Calopappus*, *Proustia vanillosma*, *Gochnatia glomeriflora*, *Perezia lanigera*, and *Onoseris stricta*). In both *Perezia* and *Leucheria* there are species with one or two rows of involucral bracts and others with the bracts in three or more rows. In *Moscharia* and *Polyachyrus* the number of bracts is reduced and dimorphic, five in *Polyachyrus* and two in *Moscharia*. In species of *Leunisia* and *Dolichlasium*, the involucral bracts are foliaceous, a phenomenon seen also in some species of *Perezia* and *Trixis*. In *Panphalea* and a few species of *Perezia* the bracts are conspicuously winged. In *Panphalea* and *Cephalopappus* the bracts are small, being less than 3 mm. long. In *Oxyphyllum*, *Perezia lanigera*, some other species of *Perezia*, and some species of *Triptilion* the involucral bracts are mucronate. As far as the involucre of the Nassauviinae are concerned, the primitive state is a monomorphic involucre with foliaceous multiseriate bracts.

Cytology. The cytology of the Mutisieae has so far been little studied.

Chromosome numbers are known for 10 per cent of the species in the tribe. The following numbers have been found: $n = 4, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20, 22, 23, 24, 25, 27,$ and 28 . The numbers most common at the level of genus are $n = 27$ and then $n = 18$. Within the subtribe Nassauviinae there are known chromosome counts for 37 of some 300 species. As our knowledge is scanty in this respect, cytological data were not used in the numerical analysis. However, there is appended a list of numbers now known for members of the Nassauviinae (TABLE 2) with some comments about the cytology of the group. In the subtribe the chromosome numbers of interest are: *Acourtia*, with $n = 27$ and 28 , and *Perezia*, with $n = 4, 8,$ and 12 , taxa which were formerly considered congeneric. The number ($n = 27$ or $2n = 54$) is found in *Acourtia*, *Trixis*, and *Proustia*. The haploid number, $n = 11$, has been found in species of genera such as *Nassauvia* and *Holocheilus*, which are not very closely related. The same is true of *Marticoenia* and *Nassauvia* where the haploid number is $n = 22$. *Moscharia* and *Leucheria* present $n = 20$.

DISCUSSION

The results of the numerical analysis permit me to make the following taxonomic conclusions, starting with the four critical taxa (a complete list of synonyms of these taxa is given in the appendices).

Gochnatia glomeriflora Gray. This is a species of small shrubs occurring on warm rocky hillsides near Guadalajara in Mexico. The flowers have 5-partite corollas and for this reason the species was ascribed to *Gochnatia* (Mutisieae, Gochnatiinae) by Gray. Sereno Watson described the same taxon as *Perezia capitata*, placed in section *Acourtia* of *Perezia*. Blake, in 1926, listed Watson's species as a synonym of Gray's *Gochnatia glomeriflora*. When Bacigalupi (1931) monographed *Acourtia*, as section *Acourtia* of *Perezia*, he neglected to include this species. Cabrera (1971a) in his monograph of *Gochnatia* excluded this species from that genus and suggested that it is an abnormal species of *Perezia*.

From the viewpoint of Aristotelian logic, the presence of 5-partite corollas is enough to exclude this species from *Acourtia*, but if all characters are considered, it is clear that this species must belong to *Acourtia*, as indeed the results of the numerical study show. There is already one species of *Acourtia*, *A. collina*, which has flowers with 5-partite corollas. The transition between 5-partite and bilabiate corollas is seen also in another genus, *Lophopappus*, of the Nassauviinae, accordingly placed very close to *Acourtia*. I conclude that this species must be placed in *Acourtia*.

Proustia vanillosma Wright. This is a species of scandent shrubs endemic to the islands of Cuba, Santo Domingo, and Puerto Rico. The only other genus of Nassauviinae occurring in this area is *Trixis*. The position of this species in *Proustia* is doubtful because of its yellow flowers, type of style, exine stratification, and its geographical distribution disjunct from other species of *Proustia* which occur in southern South America. Hoffmann (1893: 343) pointed out that *P. vanillosma* differs from the other species

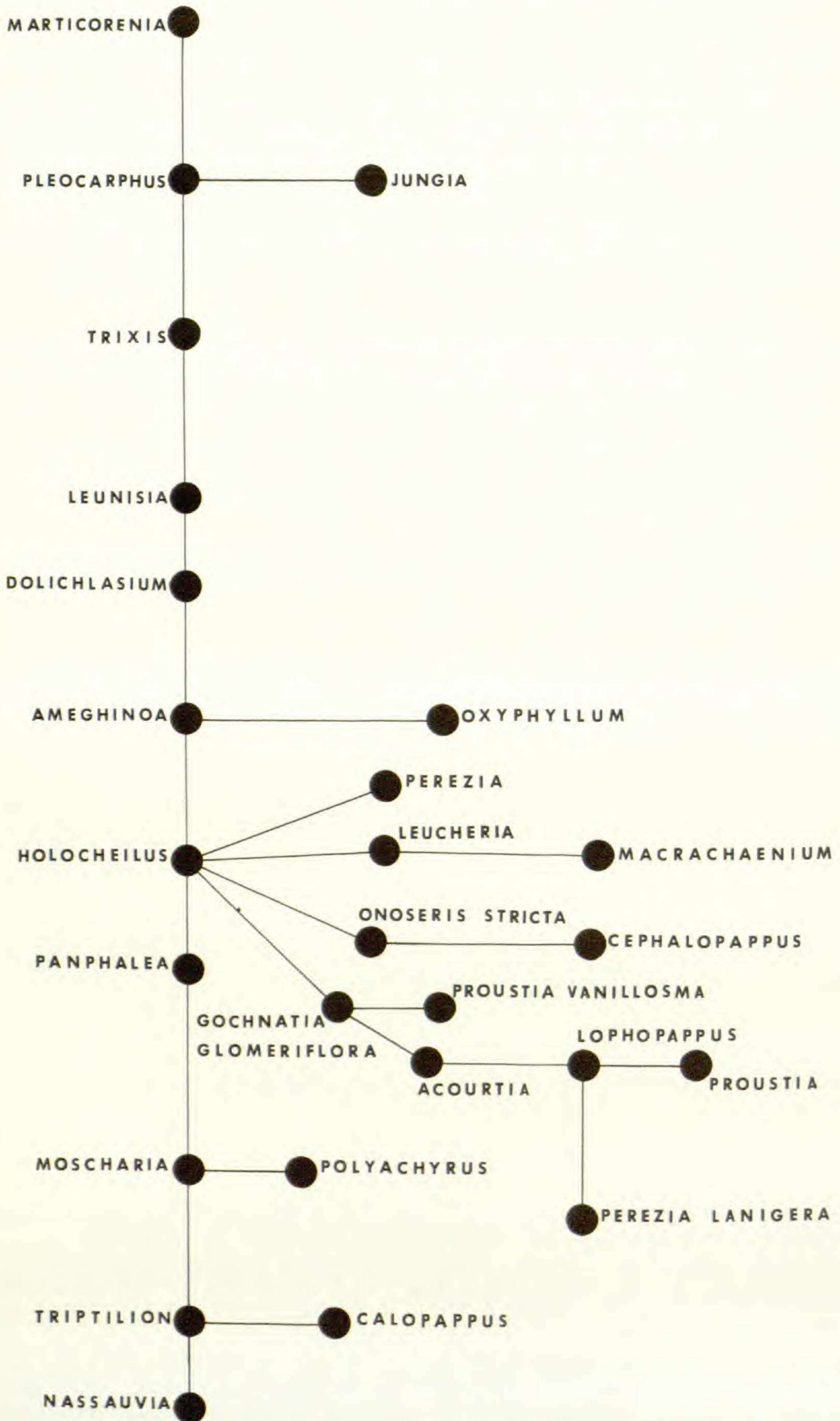


FIGURE 7. PRIM network of 26 OTU's based on TABLE 3 (Method 1).

of *Proustia* in having a different type of style. The results of the numerical study show that this taxon is close to *Acourtia glomeriflora* (= *Gochnatia glomeriflora*) and to the genus *Acourtia* in general. There is a gap between *Acourtia* and *P. vanillosma* in habit and in flower color, but the position of this species in *Acourtia* seems to be a natural one, representing a branch of this genus in the West Indies.

Perezia lanigera Hooker & Arnott. This is a species of prostrate shrubs occurring on the Patagonian steppe. B. S. Vuilleumier (1969) excluded this taxon from the genus *Perezia* because it has densely woolly trichomes in the axils of the leaves, only two rows of involucral bracts, and achenes with a type of pubescence found in no other species of *Perezia*. Cabrera (1972) replaced this species in *Perezia*; however, on the basis of the numerical study it is clear that it does not belong in that genus but seems to be related to *Lophopappus*, although the "distance" between the two taxa is fairly great. This taxon might be best treated as a new monotypic genus.

Onoseris stricta Sprengel. This is a species of perennial herbs abundant in sandy or rocky soils of Rio Grande do Sul (Brazil), Uruguay, and in northeastern Argentina. This species has "fluctuated" among genera and even subtribes, having been placed in *Trixis*, *Trichocline*, and *Perezia*. The numerical results point out that this taxon is far distant from any other in the Nassauviinae, and it might be that *O. stricta* is best placed in a subtribe other than this one. Its exact placement must await further work on the other subtribes of the Mutisieae.

From the time of Bentham and Hooker (1873) until the present, *Acourtia* has been treated as a synonym of *Perezia*. The results show that the "distance" between them is great. The gap is large enough to indicate that *Acourtia* should be treated as a distinct genus, thus confirming my preliminary decision to treat *Acourtia* as a separate OTU.

Ameghinoa and *Dolichlasium* have been treated by several authors as congeneric with *Trixis*. However the results show that the distances between them are rather large.

Pleocarphus has been treated as congeneric with *Jungia* from the time of Bentham and Hooker (1873) until now. The results show that the inclusion of *Pleocarphus* in *Jungia* is unnatural, for it produces a gap in the internal consistency of *Jungia*.

Calopappus was placed by De Candolle into another subtribe, Mutisiinae, of the tribe Mutisieae. Weddell (1855) thought it to be synonymous with *Nassauvia*. My results confirm that it is indeed a distinct genus, and it must be placed in Nassauviinae.

Holocheilus has been treated as congeneric with *Trixis* since Bentham and Hooker so placed it, but Cabrera (1968) considered *Holocheilus* to be a distinct genus and our results agree with his conclusion.

Cephalopappus, a monotypic genus, occurring only in the state of Bahia in Brazil, has been collected very few times and the only material available for this study has been the type material. The results indicate that it is far

removed from the other genera of Nassauviinae, but its inclusion in this subtribe does not seem to be unnatural.

GENERIC AFFINITIES AND EVOLUTIONARY HISTORY

In our results we have obtained a measure of phenetic resemblances. The use of these measures as an indicator of relationship or affinities can be criticized from the viewpoint of the existence of convergence or of parallelism. However, in this group we could detect neither convergence nor parallelism. For this reason we concluded that in the Nassauviinae phenetic resemblances are probably consistent with phylogenetic affinities.

On the basis of these results, the genera of the Nassauviinae can be divided into four groups and five "isolated" genera.

The first group includes *Acourtia*, *Proustia*, and *Lophopappus*. This seems to be a primitive group showing affinities with other subtribes of the Mutisieae, for in this group the styles have rounded tips and in some cases 5-partite corollas; these are characters of the Mutisiinae (sensu Cabrera, 1961). *Proustia* and *Lophopappus* are very closely related and occur in much the same area; *Acourtia* seems to represent another line of evolution in Central America and in North America.

The second group includes *Marticoenia*, *Pleocarphus*, *Jungia*, *Trixis*, *Leunisia*, *Dolichlasium*, and *Ameghinoa*. In this group there are several monotypic genera. *Marticoenia* and *Pleocarphus* seem to be closely related and the closest to these two genera is *Trixis*. *Dolichlasium* and *Leunisia* show one of the closest relationships between any genera of the Nassauviinae. *Jungia* seems to occupy a position equidistant from the other genera. This group has some characters which suggest that it is a primitive one, among them the occurrence of paleae in all flowers in *Jungia*, *Pleocarphus*, and *Marticoenia*, the shrubby habit, the many-flowered capitula, and the general occurrence of yellow flowers.

The third group includes only *Holocheilus* and *Panphalea*, and seems to have evolved from genera of the third group. This group shows some advanced characters such as the herbaceous habit, the flowers lacking pappus in *Panphalea*, and the occurrence of non-yellow flowers.

The fourth group includes *Polyachyrus*, *Moscharia*, *Triptilion*, *Nassauvia*, and *Calopappus*. It seems an advanced group, for there is a trend toward reduction of the number of flowers in each capitulum, and toward the aggregation of the capitula themselves in a capitate secondary inflorescence, a pseudocephalium. The occurrence of pseudocephalia, as compared to ordinary capitula, is thought to be an evolutionarily advanced feature. In this group are found all stages intermediate between capitula and pseudocephalia. In the genus *Moscharia* there occur pseudocephalia with a great reduction and a close aggregation of the capitula, which may be the evolutionary culmination of the trend in the Nassauviinae (Crisci, 1974b).

Nassauvia and *Triptilion* are closely related genera, and the "taxonomic distance" between them is one of the shortest between any two genera of

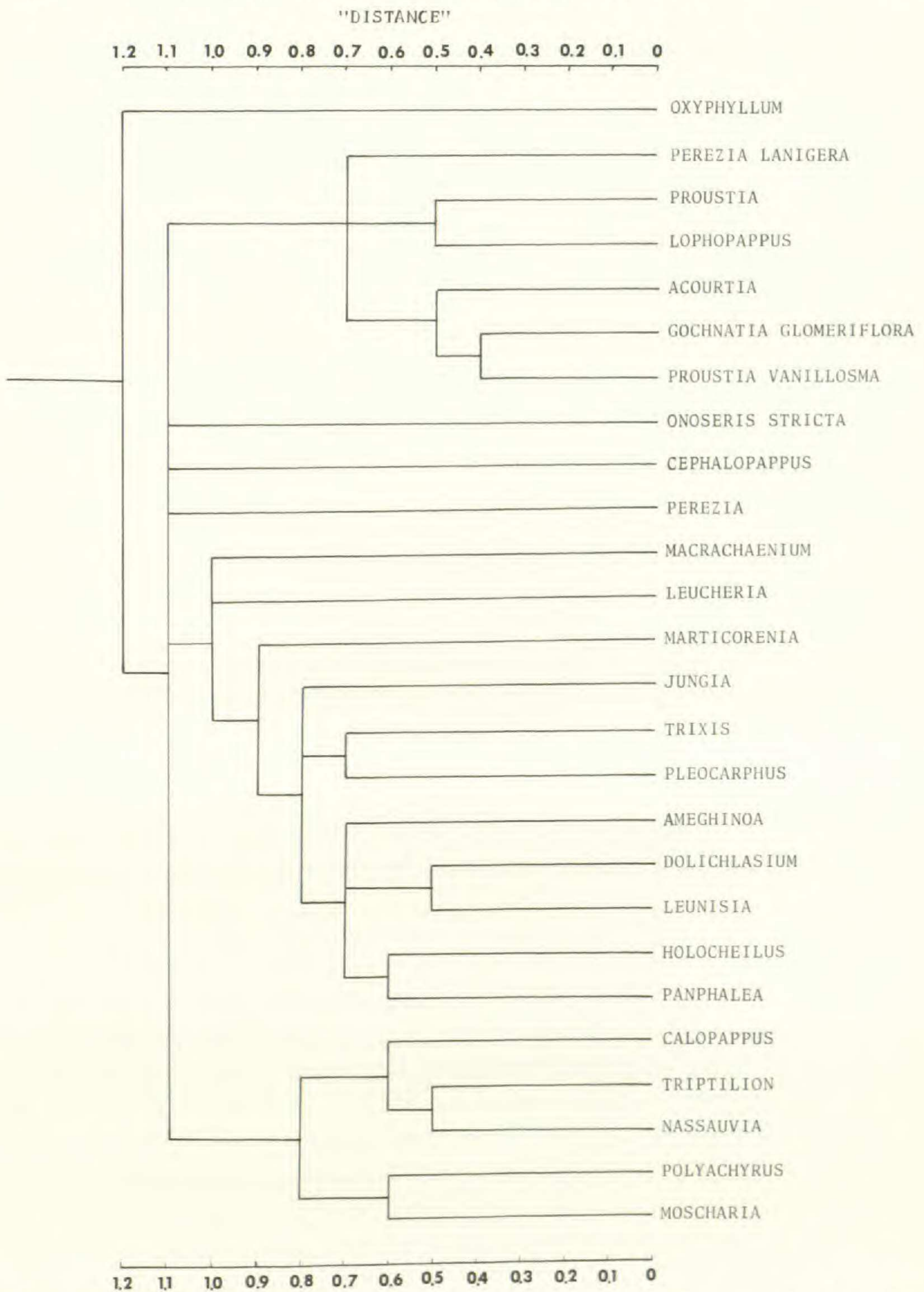


FIGURE 8. Phenogram of 26 OTU's obtained with Van Rijsbergen's clustering algorithm, based on TABLE 4 (Method 2).

the Nassauviinae. *Polyachyrus* and *Moscharia* show a clear line of evolution from *Polyachyrus* to *Moscharia*.

Throughout this study the remaining five genera have seemed isolated one from the other. Three of these, *Macrachaenium*, *Cephalopappus*, and *Oxyphyllum*, occur in areas where very few other Nassauviinae are found.

Oxyphyllum shows some very advanced features, such as few-flowered

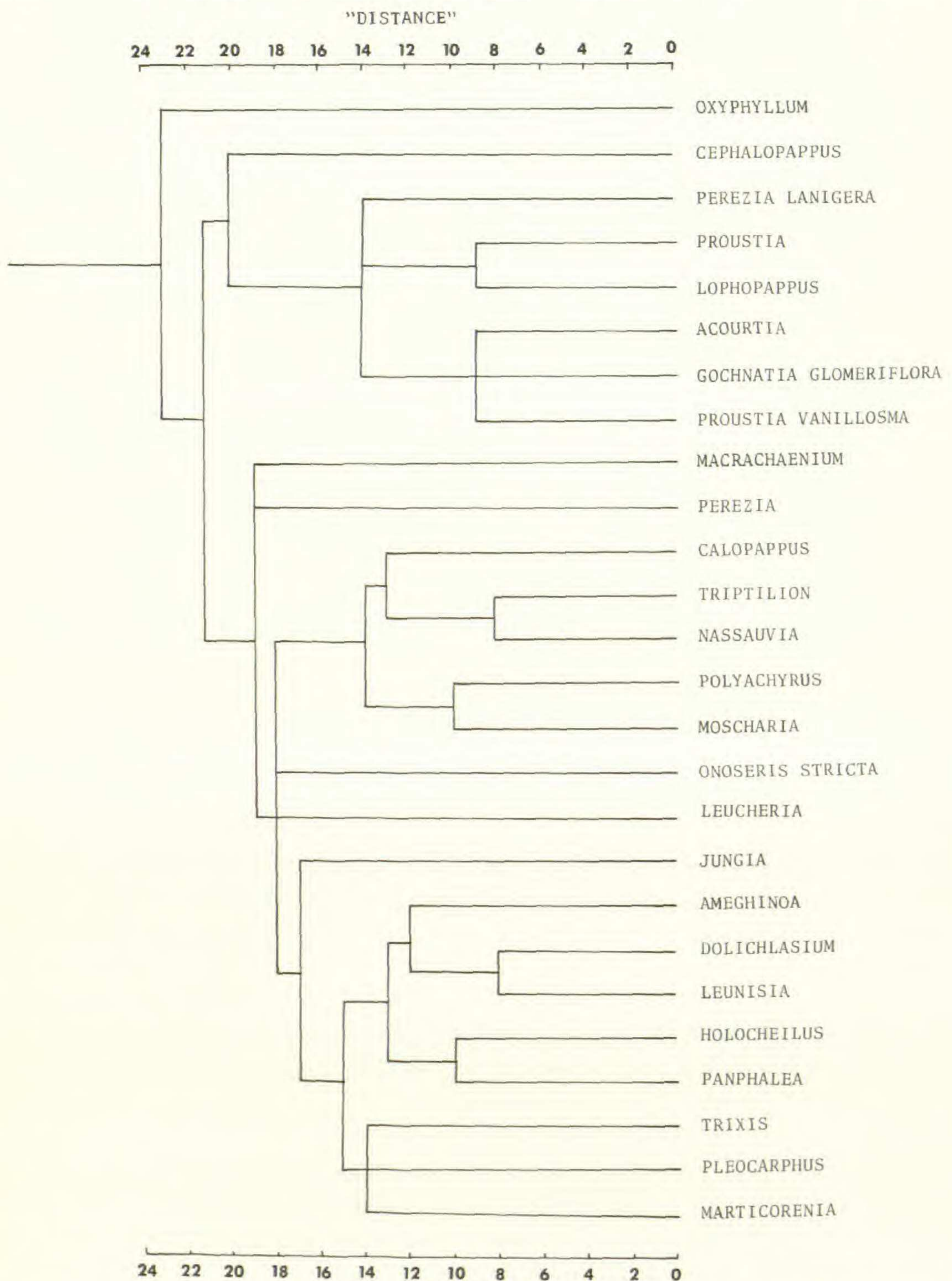


FIGURE 9. Phenogram of 26 OTU's obtained with Van Rijsbergen's clustering algorithm, based on TABLE 3 (Method 3).

capitula and a slight tendency toward aggregation of the capitula themselves, this representing an early stage in evolution of the pseudocephalium. The genus occurs in the Atacama desert of northern Chile. Its pollen resembles that of the *Moscharia* group, and it seems that this genus represents an advanced stage of development in the subtribe, the product of colonization by the Nassauviinae of a very special environment.

Macrachaenium occurs in the *Nothofagus* forest of South America. This genus shows some affinities with other subtribes of Mutisieae, for the stylar branches are rounded; it resembles *Chaptalia*, a genus of Mutisiinae. This genus might represent an evolutionary line diverging early from the other Nassauviinae and having a common ancestry with other subtribes of the Mutisieae.

Cephalopappus occurs in an area (the state of Bahia in Brazil) where there are no other genera of Nassauviinae. It displays a combination of specialized characters such as the herbaceous habit and the pappose flowers, and others less specialized such as terminal capitula. On the other hand, the stylar branches are rounded, a feature which seems to be more common in other subtribes of the Mutisieae. The position of this genus is difficult to determine, but it might be considered to represent an evolutionary line coming from an early stage in the evolution of the subtribe.

Finally, *Perezia* and *Leucheria* have been found to be isolated one from the other. This may be a result of the great spectrum of types presented by the two genera, a spectrum covering specialized and less specialized characters. These genera might have originated as two lines of development early in the evolution of the Nassauviinae.

The subtribe Nassauviinae seems to represent a natural group including several lines of evolution. Most of the genera occur in the Andean area of South America. As was pointed out by B. S. Vuilleumier (1971), the last rise of the Andes occurred in the Tertiary, and the climatic events of the Pleistocene must thus have played a decisive role in the constitution of the flora and fauna of the Andes. It is concluded that the Nassauviinae are as a group young, the product of a relatively recent evolutionary "explosion."

It seems that the Nassauviinae represent an advanced subgroup of Mutisieae. Small (1919) proposed that the Nassauviinae are the basic evolutionary group in the tribe, but our results do not agree with this idea, for it seems that the group is very young and shows advanced characters, such as the occurrence in several genera of pseudocephalia. It is possible that the Nassauviinae have originated from a taxon similar to those in the subtribe Gochnatiinae, whence, in several lines, all of the tribe Mutisieae evolved.

KEY TO THE GENERA OF SUBTRIBE NASSAUVIINAE
(Including *Onoseris stricta*)

1. Paleae in all of the flowers of the head.
 2. Lower leaves with sparse tomentose pubescence, petiolate, stipulate.
 3. Flowers yellow, pappus in more than one series; leaves linear, margin entire, revolute. PLEOCARPUS.
 3. Flowers white or pink to violet (rarely yellow), pappus in one series; leaves orbicular, cordate or broadly lanceolate, margin lobulate. JUNGIA.
 2. Lower leaves sessile, lacking tomentose pubescence, exstipulate. MARTICORENIA.

1. Paleae present only in the flowers of the margin of the heads or completely absent.
 4. Flowers without pappus.
 5. Style-branch tips rounded; capitulum solitary, receptacle pubescent. CEPHALOPAPPUS.
 5. Style-branch tips truncate; capitula disposed in cymes or panicles; receptacle glabrous. PANPHALEA.
 4. Flowers with pappus.
 6. Shrubs with leaves reduced to 3-parted spines; paleae in the marginal flowers. OXYPHYLLUM
 6. Shrubs with non-spinose leaves and capitula lacking marginal paleae, or herbs.
 7. Inflorescences in glomerula or pseudocephalia.
 8. Capitulum with 2 (rarely 3) flowers.
 9. Pseudocephalium of 7 to 9 capitula. MOSCHARIA.
 9. Pseudocephalium of more than 9 capitula. POLYACHYRUS.
 8. Capitulum of 3 to 6 flowers.
 10. Pappus formed of 4 to 5 paleae plicate along the median line expanded and laciniate in the upper part. TRIPTILION.
 10. Pappus formed of 3 to 6 paleae, narrow and not laciniate, or of setose or plumose hairs. NASSAUVIA.
 7. Capitula solitary or in cymes or panicles.
 11. Pappus palaeaceous.
 12. Flowers white or violaceous. NASSAUVIA.
 12. Flowers yellow. CALOPAPPUS.
 11. Pappus setose or plumose.
 13. Shrubs cespitose, with white flowers; Patagonia. *Perezia lanigera*.
 13. Shrubs not cespitose, flowers of various colors.
 14. Shrubs or vines; flowers yellow.
 15. Vines; involucre with more than 3 rows of bracts; plants of the West Indies. ACOURTIA (*A. vanillosma*).
 15. Shrubs; involucre with 2 rows of bracts; plants of North and South America and the West Indies.
 16. Style-branch tips rounded. LEUNISIA.
 16. Style-branch tips truncate.
 17. Receptacle pubescent. TRIXIS.
 17. Receptacle glabrous.
 18. Achenes truncate at the apex. AMEGHINOIA.
 18. Achenes with a glandular rostrum at the apex. DOLICHLASIUM.
 14. Shrubs or vines without yellow flowers, or herbs rarely with yellow flowers.
 19. Plants with a woolly pubescence.
 20. Capitulum of more than 15 flowers.
 21. Flowers orange. *Onoseris stricta*.
 21. Flowers white, blue, or violet.

22. Style-branch tips rounded, branches less than 1 mm. long.
 MACHRACHAENIUM.
22. Style-branch tips truncate or rounded, branches more than 1 mm. long.
23. Receptacle and flowers pubescent; North and Central America. ACOURTIA.
23. Receptacle and flowers glabrous; South America.
 LEUCHERIA.
20. Capitulum of fewer than 15 flowers.
24. Branches of the styles more than 1 mm. long; North America.
 ACOURTIA.
24. Branches of the styles less than 1 mm. long; South America.
25. Capitula solitary or few in number at the apex of the branches.
 LOPHOPAPPUS.
25. Capitula in panicles or racemes of spikes. PROUSTIA.
19. Plants without a woolly pubescence.
26. Involucre with 1 or 2 rows of bracts.
27. Pappus in one series. LEUCHERIA.
27. Pappus in more than one series.
 HOLOCHEILUS.
26. Involucre with more than 2 rows of bracts.
 PEREZIA.

SYNOPSIS OF THE GENERA OF NASSAUVIINAE

NASSAUVIINAE Lessing, *Linnaea* 5: 2. 1830. TYPE GENUS: *Nassauvia* Comm. ex Juss.

PLEOCARPUS D. Don in *Trans. Linn. Soc.* I. 16: 228. 1830. TYPE SPECIES: *P. revolutus* D. Don.

One shrubby species occurring in rocky soils from sea level to 900 m.s.m. in the provinces of Aconcagua, Coquimbo, and Atacama in Chile.

JUNGIA Linnaeus f., *Suppl. Pl.* 58. 1781. TYPE SPECIES: *J. ferruginosa* Linn. f.

About thirty species of shrubs or vines, rarely herbaceous, occurring in the Andean zone from northern Argentina to Mexico; also in the lowlands of Brazil.

MARTICORENIA Crisci, *Jour. Arnold Arb.* 55(1): 38-45. 1974. TYPE SPECIES: *M. foliosa* (Phil.) Crisci = *Leucheria foliosa* Philippi.

One species occurring in the Andean region of central Chile, between 32°S and 35°S and 70°W and 71°W, above timberline from 2700 to 3300 m.s.m.

CEPHALOPAPPUS Nees & Martius, *Nov. Acta Nat. Cur.* 12: 5. t. 1. 1824. TYPE SPECIES: *C. sonchifolius* Nees & Martius.

One herbaceous species occurring near the river Caxeiras (Ilheos) in the state of Bahia in Brazil; rarely collected.

PANPHALEA Lagasca, Amen. Nat. 1: 34. 1811. TYPE SPECIES: *P. commersonii* Cass.

Eight species of annual herbs occurring in southern Brazil, eastern Paraguay, Uruguay, and in northeastern Argentina.

MOSCHARIA Ruiz & Pavon, Fl. Peru. Chil. Prodr. 103. 1794. TYPE SPECIES: *M. pinnatifida* Ruiz & Pavon.

Two species of herbs occurring from Coquimbo to Maule in central Chile from sea level to ca. 2000 m.s.m.

POLYACHYRUS Lagasca, Amen. Nat. 1: 37. 1811. TYPE SPECIES: *P. poeppigii* Kunze ex Less.

About eight species, all herbaceous, occurring in central and northern Chile and in southern Peru.

TRIPTILION Ruiz & Pavon, Fl. Peru. Chil. Prodr. 102. t. 22. 1794. TYPE SPECIES: *T. spinosum* Ruiz & Pavon.

About twelve species of herbs, one occurring in Patagonia, the rest in central Chile.

NASSAUVIA Comm. ex Juss. Gen. Pl. 175. 1789. TYPE SPECIES: *N. magellanica* Gmel.

About 40 species of herbs or small shrubs occurring in the Andean zone from Malvinas Island to southern Bolivia, and in Patagonia.

CALOPAPPUS Meyen, Reise 1: 315. 1834. TYPE SPECIES: *C. acerosus* Meyen.

Two (perhaps only one) species of herbs in the Andean region of central Chile.

OXYPHYLLUM Philippi, Fl. Atacamensis 28. t 4. 1860. TYPE SPECIES: *O. ulicinum* Philippi.

One species of spinose shrubs in the Atacama desert of Chile.

ACOURTIA D. Don, Trans. Linn. Soc. I. 16: 203. 1830. TYPE SPECIES: *A. formosa* D. Don.

About 40 species of herbs or small shrubs occurring from the coastal region of southern California to El Salvador and eastward to central Texas and the West Indies. They are, for the most part, restricted to the forested middle and higher slopes of the Sierra Madre in Mexico and to the high plateaus east of the mountains in central and northern Mexico.

LEUNISIA Philippi, Linnaea 33: 120. 1864-1865. TYPE SPECIES: *L. laeta* Philippi.

One species occurring in the Andean region of central Chile (Coquimbo and Acacongua).

TRIXIS P. Browne, Civ. Nat. Hist. Jamaica 312. 1756. TYPE SPECIES: *T. inula* Crantz.

About 50 species of shrubs occurring from Mexico to central Argentina and in the West Indies. There are two centers of diversity, one in southwestern Mexico, the other in southern Brazil, northern Argentina, and Uruguay.

AMEGHINOIA Spegazzini, Rev. Fac. Agron. Vet. La Plata 3: 539. 1897. TYPE SPECIES: *A. patagonica* Spegazzini.

One shrubby species endemic to the Patagonian steppe.

DOLICHLASIUM Lagasca, Amen. Nat. 1: 33. 1811. TYPE SPECIES: *D. lagascae* D. Don.

One species of shrubby plants occurring in the Andean region of west central Argentina (provinces of La Rioja, San Juan, Mendoza, and Neuquén).

LOPHOPAPPUS Rusby emend. Cabrera, Bol. Soc. Arg. Bot. 5(1-2): 45. 1953. TYPE SPECIES: *L. foliosus* Rusby.

Five or six species of shrubs in the Andean region from Peru to northern Chile.

PROUSTIA Lagasca, Amen. Nat. 1: 33. 1811. TYPE SPECIES: *P. pyrifolia* DC.

Three species of shrubs and vines in the Andean regions of Chile, Argentina, and Bolivia.

MACRACHAENIUM Hooker f., Fl. Antarct. 2: 321. 1847. TYPE SPECIES: *M. gracile* Hook. f.

One herbaceous species endemic to the *Nothofagus* forest in southern South America.

PEREZIA Lagasca, Amen. Nat. 1: 311. 1811. TYPE SPECIES: *Perezia magellanica* (Linn. f.) Lagasca = *Perdicium magellanicum* Linn. f.

Thirty species of herbs, 27 occurring in the Andean region of South America and three in lowland open woods of Paraguay, Uruguay, Brazil, and Argentina.

LEUCHERIA Lagasca, Amen. Nat. 1: 32. 1811. TYPE SPECIES: *L. hieracioides* Cassini.

Forty-six species of herbs occurring in the Andean region from Malvinas Island to southern Peru, and in Patagonia.

HOLOCHEILUS Cassini, Bull. Sci. Soc. Philomat. 1818: 73. 1818. TYPE SPECIES: *H. brasiliensis* (Linn.) Cabrera = *H. ochroleucus* Cassini.

Six species of herbs occurring in southern Brazil, Paraguay, Uruguay, and in northern Argentina.

NOMENCLATORIAL NOTES

Acourtia vanillosma (Wright) Crisci, comb. nov.

Proustia vanillosma Wright in Sauvage, Anal. Acad. Ci. Habana 6: 212. 1860.

Perezia vanillosma (Wright) Molt. & Gómez, Anal. Soc. Hist. Nat. Madrid 19: 268. 1890.

Proustia crassinervis Urban, Symb. Antill. 1(3): 470. 1900.

Proustia krugiana Urban, *ibid.* 471.

Proustia stenophylla Urban & Ekman, Ark. Bot. 20A(5): 65. 1926.

Acourtia glomeriflora (Gray) Reveal & King, Phytologia 27: 229. 1973.

Gochnatia glomeriflora Gray, Proc. Am. Acad. 19: 57. 1883.

Perezia capitata Watson, Proc. Am. Acad. 25: 156. 1890.

Acourtia collina (Watson) Crisci, comb. nov.

Perezia collina Watson, Proc. Am. Acad. 26: 144. 1891.

Perezia lanigera Hooker & Arnott, Hook. Comp. Bot. Mag. 2: 42. 1836.

Perezia sessiliflora Spegazzini, Rev. Fac. Agron. Vet. 3: 542. 1897.

Onoseris stricta Sprengel, Linn. Syst. Veg. ed. 16. 3: 503. 1826.

Trixis stricta (Sprengel) Lessing, Linnaea 5: 25. 1830.

Trichocline heterophylla sensu Grisebach, Symb. Fl. Argent. 215. 1879, non (Sprengel) Lessing.

Perezia pampeana Spegazzini, Flora de Tandil 33. 1901.

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